

https://dspace.org/

Cognition in urban-dwelling yellow mongoose, Cynictis penicillata

Muller, Mijke

2024
University of the Witwatersrand, Johannesburg
https://hdl.handle.net/10539/37409
Muller, Mijke. (2024).Cognition in urban-dwelling yellow mongoose, Cynictis penicillata [Thesis, University of the Witwatersrand, Johannesburg]. WireDSpace. https://hdl.handle.net/10539/37409

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

Cognition in urban-dwelling yellow mongoose, *Cynictis penicillata*

MIJKE MÜLLER

Submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Faculty of Science

at the University of the Witwatersrand, Johannesburg

June 2023

DECLARATION

I hereby declare that this thesis is my own unaided work, and that recognition has been given to the references used and assistance received. It is being submitted for the Degree of Doctor of Philosophy in the Faculty of Science at the University of the Witwatersrand. It has not been submitted for any degree or examination at any other University.



……...
Mijke Müller
2 June 2023

ABSTRACT

Cognition involves perceiving and processing environmental cues and devising appropriate behavioural responses to act on the acquired information. Studying animal cognition in an urban setting provides insight into the occurrence of behavioural changes in urban-adapted animals. This thesis aimed to investigate the cognitive abilities of a population of yellow mongoose, *Cynictis penicillata*, inhabiting locations with differing extents of urbanisation in South Africa. First, I investigated whether mongooses could learn to solve a puzzle box problem of increasing complexity. The mongooses were able to solve the problem at each stage of complexity, but took longer in a residential ecological estate than those frequently visiting a residential garden. These results indicated that mongooses were capable of innovation, but their problem-solving abilities were influenced by the level of disturbance in their environment. Secondly, I investigated whether mongooses exhibited cognitive flexibility. The mongooses were able to inhibit a non-rewarding behaviour, even when it was previously rewarded, in favour of a newly rewarded behaviour during the puzzle box task. Additionally, they could solve the puzzle box problem during distraction, but took longer with the most distraction, likely splitting their attention between solving the problem and remaining vigilant. Combined, the mongooses were capable of reversal learning and divided/alternating attention, providing evidence of cognitive flexibility in this mongoose population. Thirdly, I investigated the effects of a direct human approach on the problem-solving ability of mongooses. In areas of heightened human disturbances, the mongooses had reduced tolerance to humans, but were equally efficient at solving the puzzle box problem following human disturbance than those in areas of reduced human disturbance. Those more tolerant of humans improved their problem-solving efficiency, likely adapting to the disturbance. Finally, I investigated whether mongooses experienced a paradox of choice (i.e. whether too much choice can be cognitively challenging). The mongooses in my study appeared to experience cognitive difficulties when presented with extensive choice, providing support for a paradox of choice. These results provide evidence that urban-living yellow mongooses' successful adaptation to an urban habitat may be attributed to their cognitive abilities, allowing them to exploit novel resources and flexibly adapt to the rapid environmental changes associated with urbanisation. However, the disturbance associated with urbanisation may negatively affect problem-solving efficiency, which may impact successful food acquisition, and the increased availability of resources may be cognitively challenging for urban-living yellow mongooses.

ACKNOWLEDGEMENTS

I cannot begin to express my gratitude to Professor Neville Pillay, my supervisor, advisor, and mentor, for his endless patience, guidance, faith, and support throughout this degree. Thank you for your massive amounts of confidence in me. You have encouraged me to achieve things beyond what I could have imagined. You, unknowingly, sparked my interest in animal research within the first few minutes of meeting – now eight years ago. I owe my success to you.

I am extremely grateful to everyone in the Animal Behaviour Lab for providing a helping hand, advice, and support throughout. I am especially grateful to Dr Nadine Cronk for designing the puzzle boxes used in the study, for locating the Meyersdal colonies and identifying some of the active den sites used in this study, and for her input in the experimental design of two experiments conducted in this study. A big thank you to Dr Candice Neves and Dr Megan McKay for your support and constant reassurance throughout this degree. Thank you for your assistance with navigating R's many error messages and conducting statistical analyses previously foreign to me. Thank you, Candice, for reading through the final draft of this thesis – your input is always appreciated. A special thanks to Muneera Dabhelia and Catiuscia-Jade Pinto. Thank you for your assistance in the field – you made the long days of data collection a lot easier and enjoyable. Thank you for your valuable contribution to the experimental design of the puzzle box experiments in the field. Just, thanks a bunch! I am also grateful to Megan Small and Bryony Fuller for their assistance with collecting additional data for the final experimental chapter in this thesis.

Thank you to Deon Oosthuizen, management of Meyersdal Nature Estate, Odette Campbell, management at the Meyersdal Eco Estate, and Hannes Dorfling, the chairperson of the Glenvista Renaissance Retirement Village, for allowing me to access and conduct my research at these sites. I am especially grateful for the permission to continue my field work and access my study sites despite the COVID-19 restrictions. Many thanks to Odette for taking the time to show me where active den sites were located. All my love and thanks to Oumie and Oupie for welcoming me into your home during my data collection and for your help with conducting the experiments on "die muise" in your garden.

I am thankful for the funding provided by the National Research Foundation, the PV Tobias Educational Bursary and the University of the Witwatersrand, as well as the Animal Behaviour Lab for providing me with the necessary equipment and resources I needed to conduct my study. I am also thankful to the Animal Ethics Screening Committee at the

University of the Witwatersrand for providing ethical clearance for the individual experiments conducted in this study (ethics clearance numbers: Chapter 2: AESC 2017/03/19/B; Chapter 3: AESC 2020/09/05/A; Chapter 4: AESC 2021/06/03/B; Chapter 5: AESC 2019/05/35/B). I am thankful for the assistance provided by the School of Computer Science and Applied Mathematics at the University of the Witwatersrand in developing the facial recognition software used in this study.

I am forever grateful to my family and friends for your emotional support, words of encouragement, and never-ending faith in me. Lastly, and most importantly, to my parents, Chriselle and Kobus Müller, and my sister and brother-in-law, Melineze and Jasper Christie. I would not be the person I am today, without you. Thank you for believing in me when I did not. Also, your patience is unparalleled.

I dedicate this work to those who can tell a hat from a boa constrictor digesting an elephant. I, too, was once almost convinced that it was, in fact, only a hat.

TABLE OF CONTENTS

DECLARATION ..... **i**

ABSTRACT ..... **ii**

ACKNOWLEDGEMENTS ..... **iii**

LIST OF FIGURES ..... **viii**

LIST OF TABLES ..... **xv**

CHAPTER 1: General introduction **1**

Introduction 2

The study of cognition in animals 2

Animal cognition in urban environments 4

Study species 8

Study area 9

Aim and objectives 13

Studying and identifying free-living yellow mongooses 14

Layout of thesis 15

References 15

Supplementary material 244

CHAPTER 2: Learning and innovation in urban yellow mongoose, *Cynictis penicillata* **255**

Abstract 266

Introduction 266

Materials and methods 299

Study area 299

Experimental design and protocol 30

Data analyses 344

Ethical approval 355

Results 355

Discussion 433

References 50

CHAPTER 3: Cognitive flexibility in urban yellow mongoose, *Cynictis penicillata* **566**

Abstract 577

Introduction 577

Reversal learning 588
Divided attention 60
Materials and methods 633
Study area 633
Experimental design and protocol 633
Data analyses 699
Ethical approval 699
Results 70
Reversal learning experiment 70
Attention task experiment 744
Discussion 777
References 822

CHAPTER 4: The relationship betweem flight initiation distance and cognition of urban-living yellow mongoose, *Cynictis penicillata* 899

Abstract 90
Introduction 90
Materials and methods 944
Study area 944
Experimental design and protocol 944
Data analyses 966
Ethical approval 977
Results 977
Discussion 1022
References 1077

CHAPTER 5: Do urban-living yellow mongoose, *Cynictis penicillata*, experience a paradox of choice? 1133

Abstract 1144
Introduction 1144
Materials and methods 1188
Study area 1188
Experimental design and protocol 1199
Data analyses 12020
Ethical approval 122

Results 1222
Discussion 130
References 1366

CHAPTER 6: Conclusion and recommendations 140

Discussion 141
Summary of objectives and findings 142
Cognitive abilities of urban-dwelling yellow mongooses 144
Conclusion 1477
Future direction 1499
References 150

LIST OF FIGURES

CHAPTER 1:

Figure 1. Study locations **(a)** Meyersdal Nature Estate, **(b)** Meyersdal Eco Estate, and **(c)** Glenvista Renaissance Retirement Village within the greater Meyersdal Nature Area south of Johannesburg. Inset maps of South Africa with provincial borders indicated, Gauteng province, and Johannesburg metropolitan are provided for reference. 10

Figure 2. The successful (used in the study; large green circles) and unsuccessful (excluded from the study; small yellow circles) sites within Meyersdal Nature Estate, south of Johannesburg. Only successful sites were assigned numbers: 1-5, 13. 11

Figure 3. The successful (used in the study; large green circles) and unsuccessful (excluded from the study; small blue circle) sites within Meyersdal Eco Estate, south of Johannesburg. Only successful sites were assigned numbers: 6-10, 12, and 14. 12

Figure 4. The successful site within Renaissance Retirement Home, south of Johannesburg. The number 11 was the assigned number for this site. 13

CHAPTER 2:

Figure 1. A diagram of a puzzle box used in this study. The puzzle boxes were made of transparent Perspex, allowing mongooses to visually detect food incentives. Small holes were present in the lid and sides of the box to allow mongooses to detect food incentives by smell. The boxes could be opened or closed because of two metal hinges. 30

Figure 2. Puzzle box experimental set-up of **(a)** stage 1, open stage; **(b)** stage 2, propped stage; **(c)** stage 3, closed stage; and **(d)** stage 4, impediment stage. Boxes were weighed down with rocks from the immediate environment to prevent the boxes from being moved away from the site by wind or animals..... 322

Figure 3. The latency to investigate (s) the puzzle box at **(a)** the Meyersdal Eco Estate, Meyersdal Nature Estate, and Renaissance Retirement Home and **(b)** four different stages with increasing levels of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between the three locations or the four stages. 377

Figure 4. The mean latency to consume (s) the food incentive during puzzle box experiments at **(a)** the Meyersdal Eco Estate, Meyersdal Nature Estate, and Renaissance Retirement Home and **(b)** four different stages with increasing level of complexity. Error bars indicate standard error. The same alphabet letters indicate no significant difference between the three locations or four stages. 388

Figure 5. The mean latency to consume (s) the food incentive over the various trials when solving a puzzle box problem with four stages of increasing complexity at the three different locations. 399

Figure 6. The frequency of interaction with the puzzle box before consuming the food incentive at four different stages with increasing level of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between the stages. 40

Figure 7. The frequency of interaction with the puzzle box over the various trials when solving a puzzle box problem with four stages of increasing complexity at the three different locations. 411

Figure 8. The behavioural diversity scores during interaction with the puzzles box before consuming the food incentive at four different stages with increasing level of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between the stages. 422

Figure 9. The behavioural diversity scores during interaction with the puzzle box over the various trials when solving a puzzle box problem with four stages of increasing complexity at the three different locations. 433

CHAPTER 3:

Figure 1. The experimental set-up of a reversal learning experiment conducted on yellow mongooses. **(a)** An associative learning phase where the left-most box contained the preferred food type (meat) with a small animal figurine on the lid of the box providing a visual cue, and the right-most box contained the non-preferred food type (bread) with a small pebble on the lid of the box providing a visual cue. **(b)** Reversal learning phase where the preferred and non-preferred food items were reversed so that each box contained the opposite

food item (bread left and meat right), and **(c)** a control where the orientation of the boxes is changed, the objects removed from the lids, and the placement of the two food items randomised. 677

Figure 2. The experimental set-up of an attention task experiment conducted on yellow mongooses with **(a)** zero, **(b)** one, **(c)** two, and **(d)** three distractions surrounding the puzzle box. The number of distractions surrounding the puzzle box and the position of each distraction were randomised with each trial. 688

Figure 3. The mean latency to consume (s) the preferred food item by yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate during the associative and reversal learning phases of a reversal learning experiment. 711

Figure 4. The latency (s) of yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate to contact the puzzle box containing the preferred food item during successful and unsuccessful trials at the associative learning and reversal learning phases of a reversal learning experiment. 722

Figure 5. The latency (s) of yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate to open the puzzle box containing the preferred food item during successful and unsuccessful trials at the associative learning and reversal learning phases of a reversal learning experiment. 722

Figure 6. The percentage success by yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate for each trial during the associative learning and reversal learning phases during a reversal learning experiment. 733

Figure 7. The latency to consume (s) a food incentive by yellow mongooses during puzzle box experiments with 0, 1, 2, and 3 distractions present. Error bars indicate standard error. The same alphabet letters indicate no significant difference in the number of distractions. . 744

Figure 8. The frequency of vigilance behaviour displayed by yellow mongooses at four levels of distraction during an attention task experiment. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference in the number of distractions. 755

Figure 9. The relationship between the latency to consume the food incentive and the frequency of being vigilant by yellow mongooses during an attention task experiment. The trendline is significant ($p < 0.001$; Spearman rank test). 766

CHAPTER 4:

Figure 1. (a) The mean flight initiation distance (m) during puzzle box experiments at the Meyersdal Eco Estate and Meyersdal Nature Estate. Error bars indicate standard error. **(b)** The relationship between the adjusted flight initiation distance (m) and distance to human residents (m). The trend line is significant ($p = 0.035$; Pearson's product-moment correlation). 988

Figure 2. The change in mean flight initiation distance (FID) of yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during FID experiments. The FIDs are adjusted for starting distance. 988

Figure 3. The mean distance yellow mongooses fled from the puzzle box during flight initiation (FID) experiments at the Meyersdal Eco Estate and Meyersdal Nature Estate. Error bars indicate standard error. 999

Figure 4. The change in mean distance fled (m) of yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during flight initiation distance (FID) experiments. 999

Figure 5. The mean recovery rate (s) after yellow mongooses fled from the puzzle box during flight initiation (FID) experiments at the Meyersdal Eco Estate and Meyersdal Nature Estate. Error bars indicate standard error. 100

Figure 6. The change in mean recovery rate (s) of yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during flight initiation distance (FID) experiments. 1011

Figure 7. The change in mean latency to consume (s) a food incentive by yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during flight initiation distance (FID) experiments. 1022

CHAPTER 5:

Figure 1. Cafeteria-style feeding experimental set-up with four white bowls that contained various or the same food items, presenting mongooses with a choice of food types. 1199

Figure 2. The latency to investigate the first bowl by yellow mongooses during a paradox of choice experiment in **(a)** the Meyersdal Eco Estate and Meyersdal Nature Estate during **(b)** four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.....1233

Figure 3. The latency to investigate the first bowl by yellow mongooses during a paradox of choice experiment in the Meyersdal Eco Estate (white boxes) and Meyersdal Nature Estate (grey boxes) during four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.....1244

Figure 4. The latency to consume food from the first bowl by yellow mongooses during a paradox of choice experiment in **(a)** the Meyersdal Eco Estate and Meyersdal Nature Estate during **(b)** four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments. .1255

Figure 5. The latency to consume the first food by yellow mongooses during a paradox of choice experiment in the Meyersdal Eco Estate (white boxes) and Meyersdal Nature Estate (grey boxes) during four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the

four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments. 1266

Figure 6. SAB scores for the sequence in which the bowls were investigated by yellow mongooses during a paradox of choice experiment in **(a)** the Meyersdal Eco Estate and Meyersdal Nature Estate during **(b)** four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments. 1277

Figure 7. SAB scores for the sequence in which the bowls were investigated by yellow mongooses during a paradox of choice experiment in the Meyersdal Eco Estate (white boxes) and Meyersdal Nature Estate (grey boxes) during four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments. 1288

Figure 8. Transitions when food bowls were investigated by yellow mongooses in the Meyersdal Eco Estate and the Meyersdal Nature Estate during a paradox of choice experiment. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The circles indicate bowls, and the letters A – D indicate the sequence of the four bowls (not the food types, which were randomised in the bowls). Arrows indicate a significant transition to move from one bowl to the next in the direction of the arrow. The thickness of the lines is representative of the level of significance, with thin lines being significant ($p < 0.05$) and thicker lines being highly significant ($p < 0.01$). 1299

Figure 9. Transitions when food was consumed from four bowls by yellow mongooses in the Meyersdal Eco Estate and the Meyersdal Nature Estate during a paradox of choice experiment. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The circles indicate bowls, and the letters A – D indicate the sequence of the four bowls (not the food types, which were randomised in the bowls). Arrows indicate a significant transition to move from one bowl to the next in the direction of the arrow. The thickness of the lines is representative of the level of significance, with thin lines being significant ($p < 0.05$) and thicker lines being highly significant ($p < 0.01$). 13030

LIST OF TABLES

CHAPTER 3:

Table 1. The percentage trials (number of trials/total trials) that were successful, successful with error, and unsuccessful during a control and testing phase of a reversal learning experiment.....777

CHAPTER 1

General introduction



INTRODUCTION

The study of cognition in animals

Cognition is the ability to (i) acquire new information, usually through perception, (ii) process the newly acquired information through learning, (iii) store the information in one's memory, and (iv) respond appropriately based on the acquired information through decision-making (Shettleworth, 1998). Thus, cognition involves processing information from the moment new information is received through one (or more) of the senses, to the moment a decision is made to display a particular behaviour versus another behaviour (Shettleworth, 1998; Dukas, 2002). Such cognition requires considerable energy and time investments, such as the maintenance of brain tissue (Isler and van Schaik, 2009) and neural networks (Sol et al., 2013). Various contradicting theories for enhanced cognition in animals exist. Some suggest that large brains are selected for since brain size correlates with cognition (Reader and Laland, 2002). For example, social learning, innovation, and tool use are positively correlated with brain volumes in various primate species (Reader and Laland, 2002). Others suggest that large-bodied species, with their accompanying large brains, are no better at solving tasks than small-bodied species (Benson-Amram et al., 2016), and even small-brained species, such as ants and bees, are capable of notable cognition (Chittka and Niven, 2009). More recently, it was argued, and now widely accepted, that cognition is restricted to the size of the brain relative to the body size of species (Sol et al., 2013; Benson-Amram et al., 2016). The "social brain" hypothesis further suggests that social species have enhanced cognitive abilities due to their greater social complexity (Brothers, 2002). For example, group-foraging zenaida doves, *Zenaida aurita*, are quicker at learning tasks than territorial individuals (Lefebvre and Carlier, 1996). Yet, group-living species are no more successful at solving novel tasks than solitary species (MacLean et al., 2014). Although some evidence seems to support the "social brain" hypothesis (e.g. Borrego and Dowling, 2016), others attribute enhanced cognition to ecological factors (e.g. diet, habitat, and social organisation; Bergman and Kitchen, 2009) and environmental pressures (e.g. reduced neophobia in urban animals; Guido et al., 2017). Nonetheless, the mechanism underlying cognition is debated.

The acquisition and retention of novel information allow animals to alter their behaviour (Dugatkin, 2004; Dukas, 2004), enabling innovative behavioural responses based on an animal's previous experiences with the challenges faced in their environment (Dugatkin, 2004). In this way, animals may use the new information acquired to innovatively solve novel problems that they would not have been able to solve if they had used the same

behaviour repeatedly (Ramsey et al., 2007). This, however, requires animals to behave flexibly. Phenotypic plasticity, that is, changes in individual behaviour, morphology, or physiology (Price et al., 2003), allows animals to adjust rapidly to environmental changes (Xue and Leibler, 2018). Specifically, behavioural flexibility, a characteristic of phenotypic plasticity, allows animals to adjust their behaviour rapidly, typically through learning (Sol et al., 2013). Two types of behavioural flexibility exist: expression of behaviour and development of behaviour (Sol et al., 2013). The expression of a behaviour results from a motor response caused by stimuli activating a neural network (Sol et al., 2013). This allows animals to respond rapidly to environmental changes by altering their behaviour according to their immediate needs (Sol et al., 2013). Conversely, the development of behaviour occurs through modifications of an animal's nervous system, which results in altered behavioural responses (Sol et al., 2013). This type of behavioural plasticity is more gradual, becomes permanent, and is irreversible (Sol et al., 2013). Learning is the primary mechanism for this form of behavioural plasticity (Dukas, 2004; Sol et al., 2013).

Similar to behavioural flexibility, cognitive flexibility is beneficial for survival in rapidly changing environments. Cognitive flexibility is the ability of animals to continuously acquire new information and alter their goal-directed behaviour even as the learning contingencies change (Klanker et al., 2013; Tello-Ramos et al., 2019). The terms "behavioural flexibility" and "cognitive flexibility" are often used interchangeably (Audet and Lefebvre, 2017). Behavioural flexibility is typically measured through innovative ability, the ability of an animal to solve a novel problem using previously acquired (i.e. learned) knowledge, or to solve an old problem using a new method (Ramsey et al., 2007). In contrast, experiments used to measure cognitive flexibility include, for example, reversal learning and task-switching experiments (Klanker et al., 2013; Audet and Lefebvre, 2017). For example, a key predictor of successful problem-solving is persistence, since individuals that try to solve the problem more persistently will be more likely to eventually find a solution to the problem than those that give up easily (Tebbich et al., 2010; Overington et al., 2011; Benson-Amram and Holekamp, 2012; Thornton and Samson, 2012). Yet, persistence is precisely what inhibits successful reversal learning, since persistently executing a previously learned behaviour will result in more errors when the contingencies are reversed (Audet and Lefebvre, 2017). Thus, it may be beneficial to consider cognitive flexibility, a subset of behavioural flexibility, and measure the cognitive flexibility of animals in addition to their innovative abilities and problem-solving success.

Although cognitive ability is heritable, it is not static but instead changes, particularly with environmental conditions (Sauce et al., 2018). For example, when exposing laboratory mice to increased environmental variability/novelty, Sauce et al. (2018) found that they had improved cognitive abilities (measured as performance during five different learning tasks) compared with their siblings, who were only ever exposed to sterile laboratory conditions. Similarly, the stable environment in captivity can also lead to decreased flexibility in animals (Brown et al., 2003). Thus, the rate at which an animal learns must exceed the rate of change in the environment for learning to be selected for (Dukas, 1998), and fast-changing environments must, therefore, promote fast learners.

To survive in rapidly changing environments, species must track such changes and adapt accordingly. Species with appropriate evolutionary histories, such as short generation times or individual genetic variations in traits necessary for survival, may be able to rapidly evolve genetic adaptations to keep up with the changes in their immediate environments (Sih et al., 2011). However, adaptations need not always be genetic. In a meta-analysis conducted by Hendry et al. (2008), the rates of phenotypic change were compared in animals in human-disturbed environments and more natural habitats. The rate of phenotypic change associated with such rapid changes in the human-disturbed environment exceeded that characteristic of typical environmental fluctuations (Hendry et al., 2008). Thus, most changes in phenotypes due to human-induced rapid environmental changes could be attributed to phenotypic plasticity rather than genetic adaptations (Hendry et al., 2008). This could be because the rapid environmental changes associated with human-disturbed habitats are more easily overcome through phenotypic plasticity than genetic adaptations (Hendry et al., 2008). Additionally, it has been suggested that behavioural modifications are key in allowing animals to thrive in urban environments (Sol et al., 2013) and overcome novel challenges associated with urbanisation (Price et al., 2003).

Animal cognition in urban environments

Through urbanisation, human activities result in habitat loss (Czech et al., 2000), negatively affecting biodiversity (Chace and Walsh, 2006). These areas, highly populated by humans, bring about physical changes in the environment, habitat loss, decreased species richness and diversity, as well as a change in the composition of animals occurring in these landscapes (McKinney, 2002). The rapid increase in urbanisation has impacted wildlife in various ways, resulting in species declines or a re-distribution of species attracted to, or

repelled by, urban areas (Saito and Koike, 2013). Urban wildlife encounters various shifts in their environments, such as changes in resource availability, with a reduction in natural vegetation, and natural food sources being replaced by artificial ones (McKinney, 2002, 2006). Simultaneously, there is a reduction in natural predators, but an increase in disturbances through humans and their general activities (e.g. artificial lights, noise, chemical pollution; McKinney, 2002, 2006). Although studies on urban ecology have focussed on the abovementioned effects, the impacts of urbanisation, especially on wildlife, lack attention and remain poorly understood (McKinney, 2002; Chace and Walsh, 2006). Part of the urbanisation process is the coexistence of humans and wildlife in close proximity (with subsequent increased human-wildlife interactions; Møller et al., 2013), resulting in alterations in animals' morphology, physiology, and, importantly, behaviour (Luniak, 2004; Sol et al., 2013). For instance, urban animals are typically bolder and less fearful of humans (Møller, 2009), allowing humans to approach them at shorter distances than non-urban conspecifics do (Møller et al., 2013), among other adaptations (e.g. exploiting novel food, adopting new antipredator responses, adapting to human disturbance, avoiding dangerous structures, adjusting communication in noisy environments; Sol et al., 2013).

The ecological changes associated with urbanisation are often of a large magnitude and occur rapidly, limiting the ability of wildlife to tolerate, or respond, to such changes (Hendry et al., 2008; Sih et al., 2011). Species have different tolerances to urbanisation and may respond to such environmental changes in various ways (McKinney, 2002). Urban avoiders (e.g. large-bodied ungulates such as bison, *Bison bison*, regularly persecuted species such as the wolf, *Canis lupus*, McCleery, 2010, and obligate cave roosting bat species in the family Rhinolophoidea, Marsden et al., 2023) may avoid urbanised areas altogether, and instead depend only on natural resources (Blair, 1996; McKinney, 2002). Conversely, urban exploiters (e.g. house sparrows, *Passer domesticus*, Shochat et al., 2010; house mice, *Mus mus*; black rats, *Rattus rattus*; and feral cats, *Felis catus*, McCleery, 2010) are essentially exclusively reliant on humans and the resources we provide, while urban adapters (e.g. moles, *Talpidae*; raccoons, *Procyon lotor*; foxes, *Vulpes spp*.; coyotes, *Canis laterns*, McCleery, 2010; and water mongoose, *Atilax paludinosus*, Streicher et al., 2021) are only moderate beneficiaries of urban resources (Blair 1996; McKinney, 2002). Thus, it appears as though different species have different tolerances, where some are unaffected by major human-induced environmental changes, while others are not able to tolerate such changes at all (Sol et al., 2013). The question remains: why does urbanisation have detrimental

consequences for some species, while others seem to flourish in urban settings (Sih et al., 2011; Sol et al., 2013)?

Behavioural plasticity, especially when coupled with learning, appears to be essential for surviving the challenges present in an urban environment (Sol et al., 2013). Behavioural differences exist among animals living in urban environments and conspecifics in non-urban habitats (Chapman et al., 2012; Sol et al., 2013). These behavioural differences may be a result of the improved cognitive capabilities (Byrne and Whiten, 1992; Audet et al., 2016) necessary for survival in urban areas. Comparative studies show that several species living in urban areas have enhanced cognitive capabilities compared with their rural counterparts. For example, urban bullfinches, *Loxigilla barbadensis*, are able to successfully solve puzzles to obtain a food reward much faster than rural bullfinches (Audet et al., 2016), and urban raccoons are able to open containers more successfully than their rural counterparts (MacDonald, 2015. In litt: MacDonald and Ritvo, 2016). Although these behavioural changes are necessary for survival in urban areas by aiding animals in overcoming novel challenges, the fundamental mechanisms of this adjustment are unknown (Sol et al., 2013). Conversely, some urban species, such as the house sparrow, show no improved cognitive abilities compared with their rural counterparts (Papp et al., 2015). Moreover, some evidence for reduced cognition in urban animals exists. For example, individual zenaida doves, that maintain territories in areas with higher human disturbance are slower at learning to solve a novel feeding problem than those occurring in areas with reduced human disturbance (Boogert et al., 2010). It is, therefore, important to direct more studies towards urban wildlife to gain an understanding of how the increase in the human population, and consequent urbanisation, affects the behaviour of animals, and to determine the extent to which they are adapting to urban areas.

Thus far, studies on cognition have been limited mainly to captive settings, such as laboratories and zoos, since these controlled environments allow for the manipulation of external influences, potentially affecting the accuracy of the results of such studies (Morand-Ferron et al., 2015). Similarly, decision-making experiments mainly focus on discrete decision-making, which may not be relevant in an animal's natural conditions (Yoo et al., 2021), especially when the environment or social context changes (Owen et al., 2017). This is because decision-making is not always a discrete process whereby complex behaviours, such as a predator chasing its prey, consist of individual decisions made one after the other (Yoo et al., 2021). Instead, decision-making exists on a continuum, with certain decisions occurring in a continuous manner, particularly when the outcome of one choice alters the availability of

subsequent choices (Yoo et al., 2021). However, constant decision-making may be cognitively demanding, requiring animals to simultaneously limit and process information from their environment (Budaev et al., 2019). Yet, these decision-making experiments are directed towards animals occurring in unchanging environments (Fawcett et al., 2014), neglecting decision-making in those constantly faced with rapid changes in their natural environment (e.g. urban environments). In addition to the stress linked with the capturing process, captive living conditions may result in temporary or prolonged stress that could influence cognitive abilities (Harris et al., 2008; Tello-Ramos et al., 2018). Furthermore, animals bred and kept in captive environments have been shown to have reduced behavioural flexibility and diversity compared with their free-living counterparts (e.g. Mathews et al., 2005), as well as reduced size and activity in certain brain regions compared with those in free-living conditions (Kihslinger et al., 2006). As such, experiments focused on the cognition of captive animals are not directly comparable to those in their natural habitat. Studies of human-animal interactions have primarily focused on domesticated animals, and similar studies on free-living animals are lacking, particularly those with a history of being persecuted by humans, as well as studies on the cognitive mechanisms underlying behavioural responses associated with urban living (Goumas et al., 2020).

Recently, however, there has been a rise in the appreciation for cognitive studies conducted on free-living animals that allow for minimal stress response (since no capturing process is necessary), which could otherwise potentially affect cognitive abilities (Toxopeus, et al., 2005). Yet, with this increase in interest in such studies, the number of cognitive studies on free-living animals remains a rarity (Cauchoix et al., 2017). In the present study, I considered various fundamental aspects of cognition, such as learning, cognitive flexibility, problem-solving, and decision-making in the urban-dwelling yellow mongoose, *Cynictis penicillata*. Conducting this study in an urban area allowed me to study the behaviour of a generally cryptic species, which, in this setting, is habituated to human presence and novel objects. This, in addition to the lack of interspecific competitors in urban areas, provided me with an ideal environment for studying cognition in free-living yellow mongooses. Not only does studying cognition in an urban population provide information on behaviour in an urban context, but it also provides an opportunity to study these animals that are acclimatised to humans and have little to no interference from competitors that will outcompete them for food during experiments. The cognitive mechanisms used by animals to navigate a human-altered landscape are not well-studied, yet are essential for understanding human-wildlife interactions, reducing conflict and minimising the effects of urbanisation and human

activities on urban-living animals (Goumas et al., 2020). Furthermore, no studies have considered how the increased choice of resources in urban settings may result in cognitive difficulties related to decision-making.

Study species

The yellow mongoose, *Cynictis penicillata*, is a small carnivore (Do Linh San et al., 2015) with an average body and tail length of approximately 300 mm, and a body weight ranging between 500 – 1000 g (Kingdon et al., 2013). It has a tawny to yellow-brown pelage with its tail ending in a white tip (Kingdon et al., 2013). No sexual dimorphism in size or colouration exists in this mongoose species (Kingdon et al., 2013). It is distributed throughout the semi-arid grasslands, savannas, and shrublands of southern Africa (Do Linh San et al., 2015). Yellow mongooses live in small colonies typically consisting of 8-10 individuals residing in underground burrows (Ngalo, 2014), though they are solitary foragers (Nel and Kok, 1999; le Roux et al., 2008; Manser et al., 2014). Their social groups are hierarchical in structure, with one dominant male (part of the breeding pair), several lower-ranking subordinate male and female hierarchies, and the lowest-ranking juveniles (Kingdon et al., 2013).

The yellow mongoose is diurnal, with activity being highest in the mornings between 6h00 and 12h00 (Cronk and Pillay, 2019a, 2020). Juveniles and adults are predated upon by both terrestrial and avian predators, including snakes (e.g. Cape cobra, *Naja nivea*), black-backed jackals, *Canis mesomelas*, and eagles (e.g. tawny eagles, *Aguila rapax*, martial eagle, *Polemaetus bellicosus*, and Wahlberg's eagle, *Aguila wahlbergi*; Kingdon et al., 2013). It has a generalist diet (Kingdon et al., 2013; Bizani, 2014), predominantly comprised of insects (Avenant and Nel, 1992; Nel and Kok, 1999), although it also feeds on small mammals (e.g. rodents), birds, reptiles, amphibians, eggs, and carrion (Cavallini and Nel, 1995). It is adapted to urban areas, where it lives alongside humans and exploits anthropogenic food such as garbage and chicken eggs (Cronk and Pillay, 2018, 2019a, 2019b). In a residential estate, Cronk and Pillay (2018) found that meat was the preferred food type out of six food types, and was preferred even over insects (their natural food). Moreover, anthropogenic food items such as bread were consumed regularly, and often preferred over insects and eggs (Cronk and Pillay, 2018).

Study area

This study was conducted at three locations in the Meyersdal area, south of Johannesburg, South Africa (Figure 1). The first two locations, the Meyersdal Nature Estate and the Meyersdal Eco Estate, are both ecological estates (estates that aim at protecting and conserving natural fauna and flora) separated by a double-laned tar road, which was rarely crossed by mongooses (Cronk and Pillay, 2021). Both estates are comprised of residential areas and natural grassland areas. The natural areas are dominated by two indigenous grass species: thatch grass, *Hyparrhenia hirta*, and red grass, *Themeda triandra* (Cronk and Pillay, 2018). Various bird, reptile, and mammalian species occur on these estates, with the yellow mongoose being the most prevalent mammalian carnivore (Cronk and Pillay, 2018). The third location was the Glenvista Renaissance Retirement Village, which borders both estates. A total of 20 sites (mongoose colonies) were selected for this study, 12 in the Nature Estate, seven in the Eco Estate, and one in a residential garden in the retirement home. Different sites were used for different experiments, always ensuring that at least five sites were used per location (excl. Glenvista Renaissance Retirement Village), unless it was not possible. These sites were selected based on the occurrence of yellow mongoose dens, high mongoose activity determined by frequent sightings, and a distance of at least 200 m from any other site used in a particular experiment. This ensured that individuals from separate, independent colonies were located at the various sites, based on the finding that yellow mongooses' home ranges are 0.13 km^2, on average (Cronk and Pillay, 2019a, 2021). Sites selected based on these criteria but had limited yellow mongoose activity or frequent slender mongoose, *Galerella sanguinea*, activity after experimental set-up, were classified as "unsuccessful sites" and were not used in this study. This was because slender mongooses and yellow mongooses have similar diets (Cronk and Pillay, 2019b), and slender mongooses often interfered with the experiments by consuming the food before a yellow mongoose arrived at the site (personal observations).

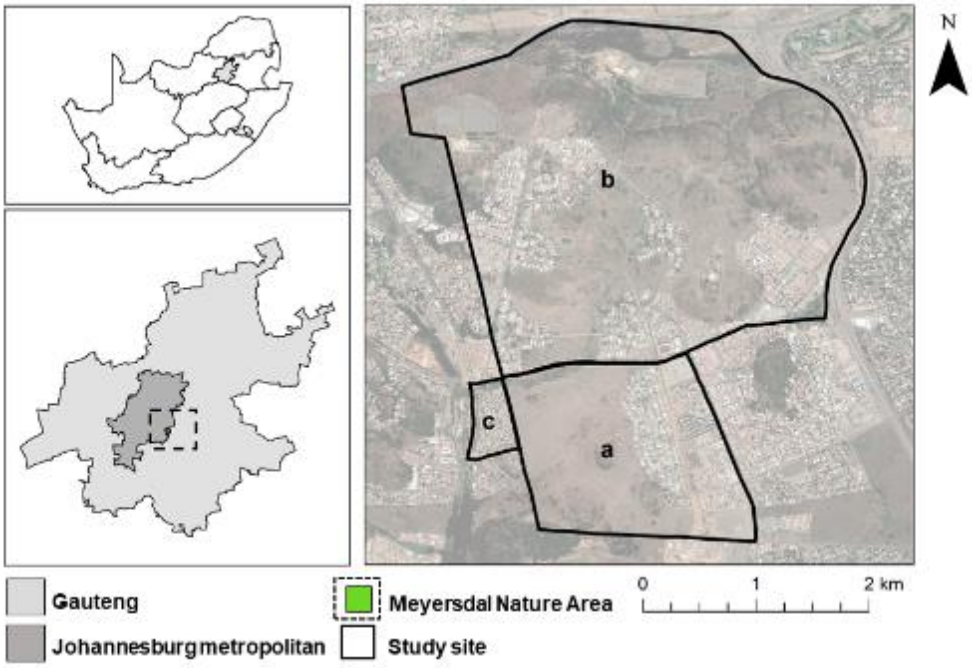


Figure 1. Study locations **(a)** Meyersdal Nature Estate, **(b)** Meyersdal Eco Estate, and **(c)** Glenvista Renaissance Retirement Village within the greater Meyersdal Nature Area south of Johannesburg. Inset maps of South Africa with provincial borders indicated, Gauteng Province, and Johannesburg metropolitan are provided for reference.

Meyersdal Nature Estate

The Meyersdal Nature Estate (26°18'08.2"S 28°04'55.9"E; 300 ha), hereafter referred to as the Nature Estate, consisted of a residential area separated from a nature area by palisade fencing. For this reason, the nature area was rarely accessed by human residents, although it was occasionally accessed by hikers, runners, and cyclists. At the time of the study, 127 bird, 28 reptilian, and five fish species had been recorded here ("Meyersdal Nature Estate," n.d.). Several game species ranging from steenbok, *Raphicerus campestris*, to eland, *Taurotragus oryx*, occurred in the area ("Meyersdal Nature Estate," n.d.). An unknown number of yellow mongoose colonies occurred in the nature area, 12 of which were selected for study (Figure 2).

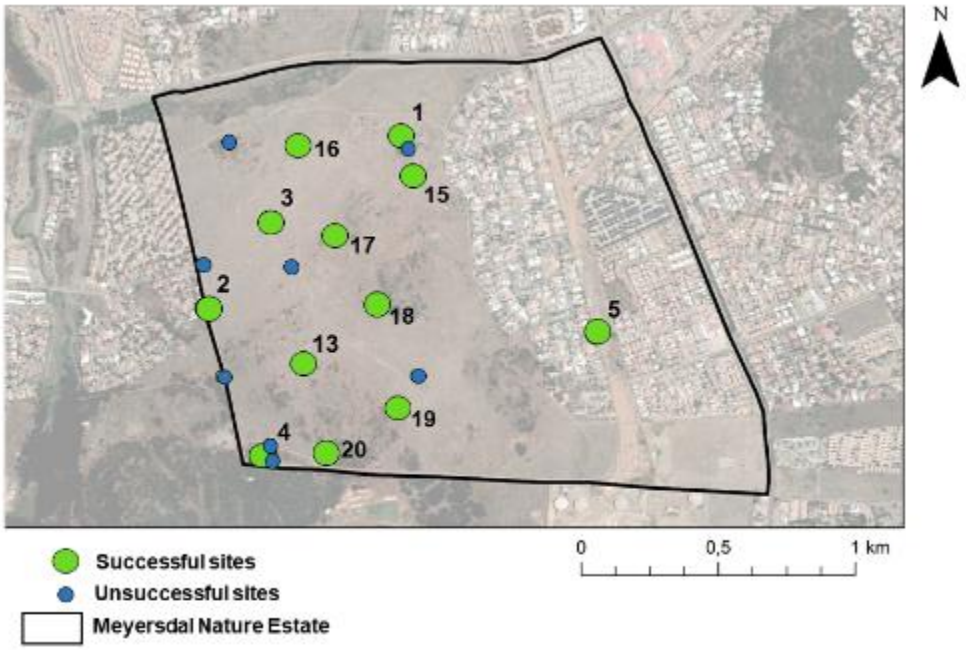


Figure 2. The successful (used in the study; large green circles) and unsuccessful (excluded from the study; small blue circles) sites within Meyersdal Nature Estate, south of Johannesburg. Only successful sites were assigned numbers: 1 – 5, 13, 15 – 20.

Meyersdal Eco Estate

The Meyersdal Eco Estate (26°17'03.6"S 28°04'50.8"E; 480 ha), hereafter referred to as the Eco Estate, is situated directly north of the Nature Estate, bordering the nature area. It consisted of residential areas interspersed throughout a nature area. Here, wildlife encountered people more frequently than those in the Nature Estate since they utilised residential gardens and travelled in-between houses. It had a wide range of wildlife, including 14 game and 98 bird species ("Meyersdal Eco - Estate," n.d.). An unknown number of yellow mongoose colonies were scattered throughout this estate, seven of which were selected for study (Figure 3).

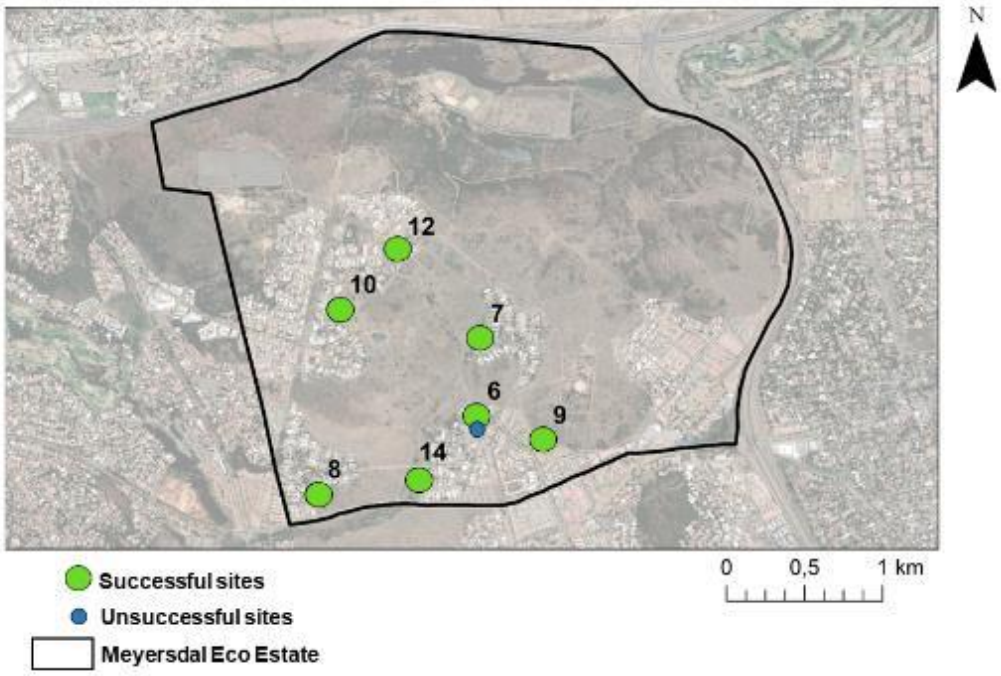


Figure 3. The successful (used in the study; large green circles) and unsuccessful (excluded from the study; small blue circle) sites within Meyersdal Eco Estate, south of Johannesburg. Only successful sites were assigned numbers: 6-10, 12, and 14.

Glenvista Renaissance Retirement Village

The Glenvista Renaissance Retirement Village (26°17'33.4"S 28°04'23.8"E; 20 ha), hereafter referred to as the Retirement Home, is located to the west of the Nature Estate and borders the nature area. In contrast to the Nature Estate and Eco Estate, the Retirement Home lacked a nature area. Thus, residential gardens with modified landscapes and non-native plant species were the only green areas within the Retirement Home. A residential garden frequently visited by yellow mongooses was selected for this study (Figure 4).

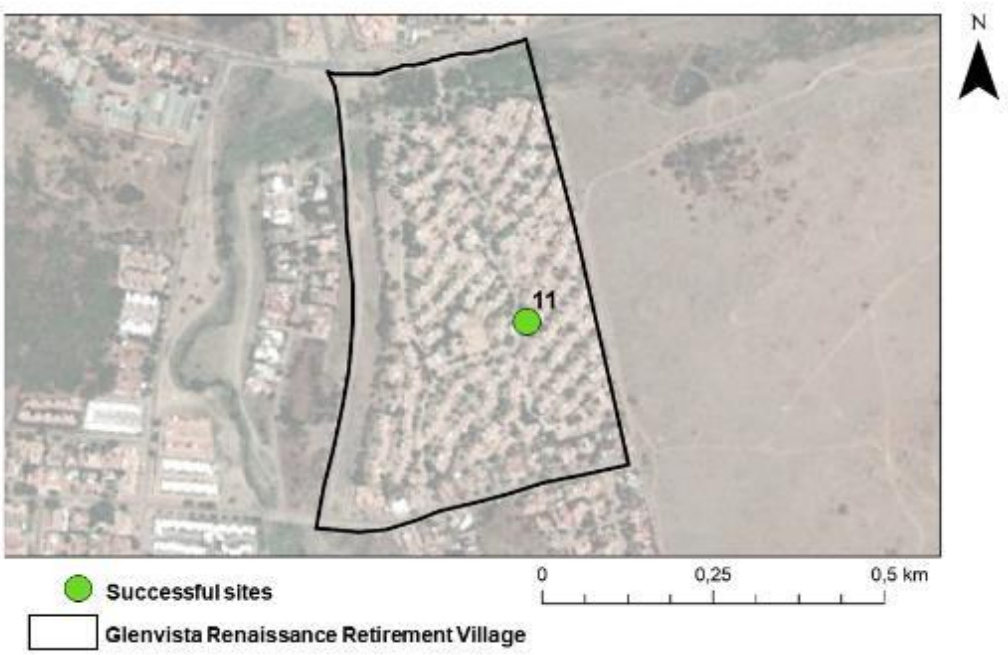


Figure 4. The successful site within Renaissance Retirement Home, south of Johannesburg. The number 11 was the assigned number for this site.

AIM AND OBJECTIVES

The primary aim of my study was to assess the cognitive abilities of yellow mongooses in an urban setting. I hypothesised that urban-dwelling yellow mongooses would display evidence of cognition when presented with different tasks. To my knowledge, the cognitive abilities of yellow mongooses have not been studied previously, particularly in an urban environment where mongooses must frequently overcome novel obstacles. Various components of cognition, including learning, problem-solving, innovation, cognitive flexibility, adaptation, and decision-making, were, therefore, assessed with a secondary component of urbanisation, and the effects of the associated human disturbances, on mongoose cognition.

The objectives of my study were to:

- assess whether yellow mongooses could learn to solve a novel problem of increasing complexity through the use of a puzzle box task,
- assess cognitive flexibility in yellow mongooses by investigating whether they are capable of reversal learning (unlearning a previously rewarded behavioural response, and learning a new, appropriate response when the learning contingencies changed) and divided attention (solving a puzzle box problem in the face of distraction),

- assess how direct human disturbance affects yellow mongooses' cognition by assessing mongooses' tolerance to human disturbance, and subsequent problem-solving efficiency after recovery from the disturbance,
- and assess whether yellow mongooses are cognitively challenged when presented with extensive food choice, thus experiencing a paradox of choice.

The abovementioned objectives included an urban component where comparisons were made among mongooses occurring in different locations, with varying levels of contact with people, and at various proximities to human residents.

STUDYING AND IDENTIFYING FREE-LIVING YELLOW MONGOOSES

My research focussed on studying cognition in free-ranging yellow mongooses in an urban area. Studying free-living wildlife is challenging since animals must interact/engage with the experimental setup (e.g. a device). I was faced with the challenges of finding study animals that occurred in sufficiently large numbers in an urbanised environment, that could habituate to my presence, at least to allow me to employ a learning device, and in an area that ensured my personal safety. The Meyersdal Estates provided such an opportunity since several yellow mongoose colonies occupied several sites in these locations, and our research lab had previously generated sufficient baseline behaviour and ecology data at these estates (Cronk and Pillay, 2018, 2019a, 2019b, 2020, 2021) to support the aims of my study. Yellow mongooses are solitary foragers (Nel and Kok, 1999; le Roux et al., 2008; Manser et al., 2014), and the home ranges of individuals from neighbouring colonies do not overlap (Cronk and Pillay, 2020). This allowed me to test how single individuals from the same colony learned the tasks needed to test their cognitive ability.

The challenge was to identify individual mongooses to track their learning and cognition. Yellow mongooses are notoriously trap-shy and, once trapped and marked, never engage with the experimental device or the trapping cage again (Cronk, personal communication). In addition, based on the negative trapping experiences for mongooses at Meyersdal, permission was not obtained from the management for further trapping and marking, especially during the COVID-19 pandemic when veterinary assistance could not be provided. I used my camera trap footage to assess whether the same individual engaged with the device throughout. However, this was only possible for individuals with an obvious morphological defect (broken tail, limp) and idiosyncratic behaviours (e.g. response towards

and interaction with the device) during the study. At the end of the study, the School of Computer Science and Applied Mathematics at the University of the Witwatersrand, Johannesburg, developed facial recognition software on high-quality photographs obtained from my camera trap footage. Using several facial markers and machine learning to identify individual mongooses (unpublished data), we were able to establish that the same individuals were continuously interacting with the device (unless otherwise stated in each experimental chapter). Overall, likelihood models showed a high facial recognition accuracy of 90.2% (confidence range: 88.1% to 97.3%), and indicated that the same mongoose per site took part and interacted with the device in studies listed in Chapters 2 – 4. For chapter 5, individual recognition was not necessarily required (see later).

LAYOUT OF THESIS

This thesis consists of 6 chapters, a general introduction (Chapter 1), four experimental chapters (Chapters 2 – 5), and conclusions and recommendations (Chapter 6). Chapter 2 is presently resubmitted after review for the journal Ethology. This work (as well as all other experimental chapters) was co-authored by my supervisor who provided general supervisory guidance and assisted with the final review and editing during manuscript preparation. However, I was the principal investigator and was responsible for the data collection, curation, formal analyses, writing of the original draft, and preparation of the chapters of the thesis. For the purpose of independence of chapters, each chapter has its own reference list resulting in the repetition of some references as well as methodological information among various chapters. The figures are numbered sequentially for each chapter, and the pages are numbered continuously for the thesis as a whole.

REFERENCES

Audet, J.-N., Ducatez, S., & Lefebvre, L. (2016). The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, *27*(2), 637–644. doi: 10.1093/beheco/arv201

Audet, J.-N., & Lefebvre, L. (2017). What's flexible in behavioral flexibility? *Behavioral Ecology*, *28*(4), 943–947. doi: 10.1093/beheco/arx007

Avenant, N. L., & Nel, J. A. J. (1992). Comparison of the diet of the yellow mongoose in a coastal and a Karoo area. *South African Journal of Wildlife Research*, *22*, 89–93.

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095. doi: 10.1098/rspb.2012.1450

Benson-Amram, Sarah, Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences*, *113*(9), 2532–2537. doi: 10.1073/pnas.1505913113

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). *Animal Cognition*, *12*(1), 63–73. doi: 10.1007/s10071-008-0171-2

Bizani, M. (2014). *Diet of the yellow mongoose (Cynictis penicillata) in the Albany Thicket Biome of South Africa* (Master of Science). University of Fort Hare.

Blair, R. B. (1996). Land Use and Avian Species Diversity Along an Urban Gradient. *Ecological Applications*, *6*(2), 506–519. doi: 10.2307/2269387

Boogert, N. J., Monceau, K., & Lefebvre, L. (2010). A field test of behavioural flexibility in zenaida doves (*Zenaida aurita*). *Behavioural Processes*, *85*(2), 135–141. doi: 10.1016/j.beproc.2010.06.020

Borrego, N., & Dowling, B. (2016). Lions (*Panthera leo*) solve, learn, and remember a novel resource acquisition problem. *Animal Cognition*, *19*(5), 1019–1025. doi: 10.1007/s10071-016-1009-y

Brothers, L. (2002). The social brain: A project for integrating primate behaviour and neurophysiology in a new domain. In J. T. Cacioppo (Ed.), *Foundations in social neuroscience* (pp. 367–386). Cambridge, Mass: MIT Press.

Brown, C., Davidson, T., & Laland, K. (2003). Environmental enrichment and prior experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon: Environmental enrichment improves foraging. *Journal of Fish Biology*, *63*, 187–196. doi: 10.1111/j.1095-8649.2003.00208.x

Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S., & Giske, J. (2019). Decision-Making From the Animal Perspective: Bridging Ecology and Subjective Cognition. *Frontiers in Ecology and Evolution*, *7*, 164. doi: 10.3389/fevo.2019.00164

Byrne, R. W., & Whiten, A. (1992). Cognitive Evolution in Primates: Evidence from Tactical Deception. *Man*, *27*(3), 609. doi: 10.2307/2803931

Cauchoix, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field: Comparison of reversal learning performance in captive and wild passerines. *Scientific Reports*, *7*(1), 12945. doi: 10.1038/s41598-017-13179-5

Cavallini, P., & Nel, J. A. J. (1995). Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). *South African Journal of Zoology*, *30*(2), 46–49. doi: 10.1080/02541858.1995.11448371

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, *74*, 46–69. doi: 10.1016/j.landurbplan.2004.08.007

Chapman, T., Rymer, T., & Pillay, N. (2012). Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris*. *Naturwissenschaften*, *99*(11), 893–902. doi: 10.1007/s00114-012-0971-8

Chittka, L., & Niven, J. (2009). Are bigger brains better? *Current Biology*, *19*(21), R995–R1008. doi: 10.1016/j.cub.2009.08.023

Cronk, N. E., & Pillay, N. (2018). Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethologica*, *21*(2), 127–136. doi: 10.1007/s10211-018-0291-x

Cronk, N. E., & Pillay, N. (2019a). Flexible use of urban resources by the yellow mongoose *Cynictis penicillata*. *Animals*, *9*(7), 447. doi: 10.3390/ani9070447

Cronk, N. E., & Pillay, N. (2020). Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment. *Journal of Urban Ecology*, *6*(1), 1–9. doi: 10.1093/jue/juaa013

Cronk, N. E., & Pillay, N. (2021). Home range and use of residential gardens by yellow mongoose *Cynictis penicillata* in an urban environment. *Urban Ecosystems*, *24*(1), 127–139. doi: 10.1007/s11252-020-01022-1

Cronk, N., & Pillay, N. (2019b). Dietary overlap of two sympatric African mongoose species in an urban environment. *Mammalia*, *85*(5), 428–438. doi: 10.1515/mammalia-2018-0113

Czech, B., Krausman, P. R., & Devers, P. K. (2000). Economic associations among causes of species endangerment in the United States. *BioScience*, *50*(7), 593. doi: 10.1641/0006-3568(2000)050[0593:EAACOS]2.0.CO;2

Do Linh San, E., Cavallini, P., & Taylor, P. (2015). *The IUCN Red List of Threatened Species 2015* [Data set]. International Union for Conservation of Nature. doi: 10.2305/IUCN.UK.2015-4.RLTS.T41597A45205726.en

Dugatkin, L. A. (2004). *Principles of animal behavior*. New York: W.W. Norton & Company.

Dukas, R. (Ed.). (1998). Evolutionary ecology of learning. In *Cognitive ecology: The evolutionary ecology of information processing and decision making* (pp. 129–174). Chicago: University of Chicago Press.

Dukas, R. (2002). Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1539–1547. doi: 10.1098/rstb.2002.1063

Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 347–374. doi: 10.1146/annurev.ecolsys.35.112202.130152

Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C., & McNamara, J. M. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences*, *18*(3), 153–161. doi: 10.1016/j.tics.2013.12.012

Goumas, M., Lee, V. E., Boogert, N. J., Kelley, L. A., & Thornton, A. (2020). The role of animal cognition in human-wildlife interactions. *Frontiers in Psychology, 11*, 589978. doi: 10.3389/fpsyg.2020.589978

Guido, J. M., Biondi, L. M., Vasallo, A. I., & Muzio, R. N. (2017). Neophobia is negatively related to reversal learning ability in females of a generalist bird of prey, the Chimango Caracara, *Milvago chimango*. *Animal Cognition, 20*(4), 591–602. doi: 10.1007/s10071-017-1083-9

Harris, A. P., D'eath, R. B., & Healy, S. D. (2008). Sex differences, or not, in spatial cognition in albino rats: Acute stress is the key. *Animal Behaviour, 76*(5), 1579–1589. doi: 10.1016/j.anbehav.2008.07.016

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*(1), 20–29. doi: 10.1111/j.1365-294X.2007.03428.x

Isler, K., & van Schaik, C. P. (2009). The expensive brain: A framework for explaining evolutionary changes in brain size. *Journal of Human Evolution*, *57*(4), 392–400. doi: 10.1016/j.jhevol.2009.04.009

Kihslinger, R. L., Lema, S. C., & Nevitt, G. A. (2006). Environmental rearing conditions produce forebrain differences in wild Chinook salmon *Oncorhynchus tshawytscha*. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *145*(2), 145–151. doi: 10.1016/j.cbpa.2006.06.041

Kingdon, J., Happold, D., Butynski, T., Hoffman, M., Happold, M., & Kalina, J. (Eds.). (2013). *Cynictis penicillata*, Yellow Mongoose. In *Mammals of Africa. Vol. 5: Carnivores, pangolins, equids and rhinoceroses* (pp. 334–339). London: Bloomsbury.

Klanker, M., Feenstra, M., & Denys, D. (2013). Dopaminergic control of cognitive flexibility in humans and animals. *Frontiers in Neuroscience*, *7*. doi: 10.3389/fnins.2013.00201

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behaviour*, *75*(3), 943–949. doi: 10.1016/j.anbehav.2007.07.014

Lefebvre, L., & Carlier, P. (1996). Differences in individual learning between group-foraging and territorial zenaida doves. *Behaviour*, *133*(15–16), 1197–1207. doi: 10.1163/156853996X00369

Luniak, M. (2004). Synurbization-adaptation of animal wildlife to urban development. In W. W. Shaw, L. K. Harris, & L. VanDruff (Eds.), *Proceedings of the 4th International Symposium on Urban Wildlife Conservation* (pp. 50–55). University of Arizona.

MacDonald, S. E., & Ritvo, S. (2016). Comparative cognition outside the laboratory. *Comparative Cognition & Behavior Reviews*, *11*, 49–61. doi: 10.3819/ccbr.2016.110003

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., … Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences*, *111*(20), E2140–E2148. doi: 10.1073/pnas.1323533111

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal Complexity in Meerkats and Other Mongoose Species. *Advances in the Study of Behavior*, *46*, 281–310. doi: 10.1016/B978-0-12-800286-5.00006-7

Mathews, F., Orros, M., McLaren, G., Gelling, M., & Foster, R. (2005). Keeping fit on the ark: Assessing the suitability of captive-bred animals for release. *Biological Conservation*, *121*(4), 569–577. doi: 10.1016/j.biocon.2004.06.007

McCleery, R. A. (2010). Urban Mammals. In J. Aitkenhead-Peterson & A. Volder (Eds.), *Urban Ecosystem Ecology* (pp. 87–102). American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Marsden, G. E., Vosloo, D., & Schoeman, M. C. (2023). Urban tolerance is phylogenetically constrained and mediated by pre-adaptations in African bats. Ecology and Evolution, *13*(3), e9840. doi: 10.1002/ece3.9840

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience*, *52*(10), 883–890. doi: 10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. doi: 10.1016/j.biocon.2005.09.005

Meyersdal Eco—Estate. (n.d.). Retrieved March 10, 2019, from https://www.meyersdaleco.co.za/

Meyersdal Nature Estate. (n.d.). Retrieved March 10, 2019, from https://www.natureestate.co.za/

Møller, A. P. (2009). Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, *159*(4), 849–858. doi: 10.1007/s00442-008-1259-8

Møller, A. P., Grim, T., Ibanez-Alamo, J. D., Marko, G., & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, *24*(5), 1211–1217. doi: 10.1093/beheco/art054

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: Associative learning in wild great tits. *PLOS ONE*, *10*(8), e0133821. doi: 10.1371/journal.pone.0133821

Nel, J. A. J., & Kok, O. B. (1999). Diet and foraging group size in the yellow mongoose: A comparison with the suricate and the bat-eared fox. *Ethology Ecology & Evolution*, *11*(1), 25–34. doi: 10.1080/08927014.1999.9522839

Ngalo, S. (2014). Yellow mongoose—SANBI. Retrieved March 28, 2018, from https://www.sanbi.org/animal-of-the-week/yellow-mongoose/

Overington, S. E., Cauchard, L., Côté, K.-A., & Lefebvre, L. (2011). Innovative foraging behaviour in birds: What characterizes an innovator? *Behavioural Processes*, *87*(3), 274–285. doi: 10.1016/j.beproc.2011.06.002

Owen, M. A., Swaisgood, R. R., & Blumstein, D. T. (2017). Contextual influences on animal decision-making: Significance for behavior-based wildlife conservation and management. *Integrative Zoology*, *12*(1), 32–48. doi: 10.1111/1749-4877.12235

Papp, S., Vincze, E., Preiszner, B., Liker, A., & Bókony, V. (2015). A comparison of problem-solving success between urban and rural house sparrows. *Behavioral Ecology and Sociobiology*, *69*(3), 471–480. doi: 10.1007/s00265-014-1859-8

Price, T. D., Qvarnström, A., & Irwin, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1523), 1433–1440. doi: 10.1098/rspb.2003.2372

Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, *30*(04), 393 –437. doi: 10.1017/S0140525X07002373

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*(7), 4436–4441. doi: 10.1073/pnas.062041299

Saito, M., & Koike, F. (2013). Distribution of wild mammal assemblages along an urban–rural–forest landscape gradient in warm-temperate East Asia. *PLoS ONE*, *8*(5), e65464. doi: 10.1371/journal.pone.0065464

Sauce, B., Bendrath, S., Herzfeld, M., Siegel, D., Style, C., Rab, S., … Matzel, L. D. (2018). The impact of environmental interventions among mouse siblings on the heritability and malleability of general cognitive ability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170289. doi: 10.1098/rstb.2017.0289

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., & Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, *60*(3), 199–208. doi: 10.1525/bio.2010.60.3.6

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change: Behaviour and evolution. *Evolutionary Applications*, *4*(2), 367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Streicher, J. P., Ramesh, T., & Downs, C. T. (2021). An African urban mesocarnivore: Navigating the urban matrix of Durban, South Africa. Global Ecology and Conservation, 26, e01482. doi: 10.1016/j.gecco.2021.e01482

Tebbich, S., Sterelny, K., & Teschke, I. (2010). The tale of the finch: Adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1543), 1099–1109. doi: 10.1098/rstb.2009.0291

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: To be or not to be flexible, that is the question. *Animal Behaviour*, *147*, 129–136. doi: 10.1016/j.anbehav.2018.02.019

Tello-Ramos, M. C., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., & Pravosudov, V. V. (2018). Memory in wild mountain chickadees from different elevations: Comparing first-year birds with older survivors. *Animal Behaviour*, *137*, 149–160. doi: 10.1016/j.anbehav.2017.12.019

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468. doi: 10.1016/j.anbehav.2012.03.018

Toxopeus, I. B., Sterck, E. H. M., van Hooff, J. A. R. A. M., Spruijt, B. M., & Heeren, T. J. (2005). Effects of trait anxiety on performance of socially housed monkeys in a learning test. *Behaviour*, *142*(9–10), 1269–1287. doi: 10.1163/156853905774539373

Xue, B., & Leibler, S. (2018). Benefits of phenotypic plasticity for population growth in varying environments. *Proceedings of the National Academy of Sciences*, *115*(50), 12745–12750. doi: 10.1073/pnas.1813447115

Yoo, S. B. M., Hayden, B. Y., & Pearson, J. M. (2021). Continuous decisions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1819), 20190664. doi: 10.1098/rstb.2019.0664

SUPPLEMENTARY MATERIAL

Table S1. The sites used throughout this study with its location, proximity to nearest residents (m), the experiment and chapter in which it was used (Y for yes, N for no), the starting distance during the FID experiment if it was utilised, and the bowl configuration during the paradox of choice experiment.

Location	Site	Proximity to nearest human residents (m)	Experiment (Chapter)				
			Learning (Ch. 1)	Reversal Learning (Ch. 2)	Divided Attention (Ch. 2)	FID (Ch. 3)/ Starting distance (m)	Paradox of Choice (Ch. 4)
Meyersdal Nature Estate	1	147	Y	Y	Y	Y/10	N
	2	<10	Y	Y	Y	N	N
	3	278	Y	Y	Y	N	N
	4	115	Y	Y	Y	N	N
	5	32	Y	N	N	Y/10	N
	13	434	N	Y	Y	Y/20	N
	15	105	N	N	N	N	Y
	16	351	N	N	N	N	Y
	17	414	N	N	N	N	Y
	18	314	N	N	N	N	Y
	19	450	N	N	N	N	Y
	20	333	N	N	N	N	Y
Meyersdal Eco Estate	6	20	Y	Y	Y	N	Y
	7	32	Y	Y	Y	Y/20	Y
	8	17	Y	Y	Y	N	Y
	9	<10	Y	Y	Y	N	Y
	10	69	Y	N	N	N	N
	12	<10	N	Y	Y	N	Y
	14	<10	N	N	N	Y/20	Y
Glenvista Renaissance Retirement Village	11	0	Y	N	N	N	N

CHAPTER 2

Learning and innovation in urban yellow mongoose, *Cynictis penicillata*

Mijke Müller, Neville Pillay

Resubmitted after review to the journal
Ethology



ABSTRACT

Problem-solving and innovation have been studied extensively, yet urban animals are overlooked in such studies despite having opportunities to innovate in urban areas. I studied problem-solving in yellow mongooses, *Cynictis penicillata*, in an urban setting in South Africa. Using novel puzzle box experiments, I investigated whether yellow mongooses could solve a task of increasing complexity in three locations with varying extents of anthropogenic interactions. Mongooses in a residential ecological estate took the longest time to solve the problem, whereas those frequenting a residential garden solved the problem the fastest. Mongooses solved the puzzle box problem at each of the four stages of complexity, but were the fastest during the least complex first stage, followed by the third stage, and requiring more time in the second and fourth stages of complexity. Overall, the location of the mongoose colonies and the complexity of the task were the main correlates of the speed of solving the problem. Urban-living yellow mongooses can interact with novelty in an anthropogenic environment and solve novel problems through innovation to obtain a food incentive.

Keywords: *anthropogenic, carnivore, cognition, novelty, problem-solving, puzzle box*

INTRODUCTION

Learning is a cognitive process through which animals acquire information regarding novelties in their environment and then use this information to adjust their behaviour accordingly (Dugatkin, 2004; Dukas, 2004). This allows for innovative behavioural responses, based on an animal's previous experiences with the challenges faced in their environment (Dugatkin, 2004). In this way, animals may use the new information acquired to innovatively solve novel problems that they would not have been able to solve if they had used the same behaviour repeatedly (Ramsey et al., 2007).

Problem-solving success and innovative behaviour have been attributed to various factors, such as reduced neophobia, increased exploratory behaviour, and behavioural persistence (Biondi et al., 2010). Various studies show that these factors are consistent across various taxa. For example, Biondi et al. (2010) attributed the ecological success of chimango caracara, *Milvago chimango*, to its low neophobia and highly explorative behaviour. In a comparative study, enhanced cognition in chacma baboons, *Papio ursinus*, was attributed to lower neophobic tendencies and greater explorative nature compared with gelada baboons, *Theropithecus gelada* (Bergman and Kitchen, 2009). In red fronted lemurs, *Eulemur*

rufifrons, persistence (i.e. consistent trying) is the most important factor for successfully solving an artificial feeding puzzle through innovation (Huebner and Fichtel, 2015). Several mammalian carnivores also follow the same trend. For example, problem-solving success has been attributed to exploration, greater persistence, and low neophobia in raccoons, *Procyon lotor* (Daniels et al., 2019) and spotted hyaenas, *Crocuta crocuta* (Benson-Amram and Holekamp, 2012; Johnson-Ulrich et al., 2018), whereas innovation in meerkats, *Suricata suricatta*, is often a result of exploration, persistence, and learning (Thornton and Samson, 2012).

Thus far, studies on cognition have been largely limited to captive settings such as laboratories and zoos, since these controlled environments allow for the experimental manipulation of external influences (e.g. predation, food availability) that could potentially affect the accuracy of the results of such studies (Morand-Ferron et al., 2015). However, there has been a rise in the appreciation for cognitive studies in free-living animals (e.g. Benson-Amram and Holekamp, 2012; Morand-Ferron et al., 2015; Pritchard et al., 2016; Ashton et al., 2018). Furthermore, although several studies have considered the underlying mechanisms of problem-solving and innovation (e.g. Boogert et al., 2010; Benson-Amram and Holekamp, 2012; Thornton and Samson, 2012), relatively few have considered this in an urban setting despite the increased opportunity for animals to innovate in urban areas.

In urban areas, animals face unusual challenges that often require problem-solving. For example, the innovative opening of dustbins and bags to feed on human garbage has been observed in keas, *Nestor notabilis* (Gajdon et al., 2006), chimango caracara (Biondi et al., 2010), raccoons (Isabella, 2016), and more recently, sulphur-crested cockatoos, *Cacatua galerita*, (Klump et al., 2022). These urban-dwelling animals are exposed to more novel food sources and fewer natural predators (McKinney, 2002, 2006; Sol et al., 2013). As a result, urban animals tend to have reduced neophobia and are typically more explorative, factors that are considered predictors of innovativeness (Prasher et al., 2019). The urban context provides a unique opportunity for studies of problem-solving in free-living animal populations. This is especially important for cryptic species since they are habituated to human presence and novel objects in an urban setting.

I studied problem-solving and innovation in an urban population of yellow mongoose, *Cynictis penicillata*, a small carnivore (500 – 1000 g; Kingdon et al., 2013) distributed throughout the semi-arid grasslands, savannas, and shrublands of southern Africa (Do Linh San et al., 2015). It lives in small colonies typically consisting of 8-10 individuals residing in underground burrows (Ngalo, 2014), but usually forages individually (le Roux et al., 2008;

Manser et al., 2014). It has a generalist diet (Kingdon et al., 2013) predominantly comprised of insects (Avenant and Nel, 1992; Nel and Kok, 1999), although it also feeds on small mammals (e.g. rodents), birds, reptiles, amphibians, eggs, and carrion (Cavallini and Nel, 1995; Cronk and Pillay, 2018, 2019a, 2019b). It is somewhat common in urban areas, where it ingests anthropogenic food (e.g. garbage, such as plastic, and chicken eggs; Cronk and Pillay, 2019a; 2019b). In a residential estate, Cronk and Pillay (2018) used cafeteria feeding trials with six different food types and found that the mongooses preferred deli meat over insects (their natural food). Moreover, anthropogenic food items, such as bread, were consumed regularly and often preferred over insects and eggs (Cronk and Pillay, 2018).

The aim of my study was to investigate whether urban-occurring yellow mongooses could learn to solve a novel task involving puzzle boxes containing a food incentive. I increased the complexity of the puzzle box tasks in four sequential stages, ranging from an open box, to a slightly open box, to a closed box, and finally to a closed box with an impediment. I tested yellow mongooses in three settings based on their proximity to human residences: a natural area with minimal human contact, a residential area with intermediate human contact, and a residential garden with frequent human contact. I expected that mongooses would quickly habituate to the boxes because of reduced neophobia (pilot observations), but that mongooses in closer proximity to humans would be less neophobic than those in areas with less human contact. I predicted that yellow mongooses would solve the puzzle boxes at all stages but that they would take longer to complete tasks at the more complex stage because it would require more time to open the box. I also predicted behavioural persistence and enhanced exploratory behaviour at more complex stages if the mongooses succeeded in solving the tasks, since animals with increased persistence and exploration are more likely to successfully solve novel problems (Benson-Amram and Holekamp, 2012; Benson-Amram et al., 2013; Johnson-Ulrich et al., 2018). Finally, I predicted that, because of their reduced neophobia, mongooses in closer proximity to humans would be able to solve the puzzle box problem faster as a result of their quicker engagement with the puzzle box (Benson-Amram and Holekamp, 2012; Benson-Amram et al., 2013). No a priori predictions were made for potential differences in persistence and exploratory behaviour between the three locations.

MATERIALS AND METHODS

Study area

This study was conducted at three locations in the Meyersdal area, south of Johannesburg, South Africa. The first two locations, the Meyersdal Nature Estate and the Meyersdal Eco Estate, were both ecological estates that aimed at protecting and conserving natural fauna and flora. They were separated by a tarred multi-lane motorway, which the mongooses rarely crossed (Cronk and Pillay, 2021). Yellow mongooses were the most prevalent mammalian carnivore in the estates (Cronk and Pillay, 2018). The Meyersdal Nature Estate (26°18'08.2"S 28°04'55.9"E; 300 ha), hereafter referred to as the Nature Estate, consisted of a residential area separated from a nature area by palisade fencing. For this reason, the nature area was rarely accessed by human residents, although it was accessed by hikers, runners and cyclists occasionally. The Meyersdal Eco Estate (26°17'03.6"S 28°04'50.8"E; 480 ha), hereafter referred to as the Eco Estate, was situated directly north of the Nature Estate, bordering the nature area. It consisted of residential areas interspersed throughout a nature area. Here, wildlife encountered people more frequently than those in the Nature Estate since they used residential gardens and travelled between houses. The third location was the Glenvista Renaissance Retirement Village (26°17'33.4"S 28°04'23.8"E; 20 ha), hereafter referred to as the Retirement Home, which bordered both estates. In contrast to the Nature Estate and the Eco Estate, the Retirement Home lacked a nature area, but mongooses frequently foraged in residential gardens and were fed by residents. A total of 11 sites (colonies) were selected for this study: five in the Nature Estate (mean straight-line distance to nearest human residence: 116.4 m; measured using Google Earth™); five in the Eco Estate (mean straight-line distance to the nearest human residence: 29.6 m); and one in a residential garden in the Retirement Home as sampling here was opportunistic, and only one site was located (straight-line distance to the human residence: 0 m). The individual sites within the estates were selected based on the occurrence of yellow mongoose dens, high mongoose activity determined by frequent sightings, and a distance of at least 200 m from any other site. This ensured that individuals from separate, independent colonies occurred at the various sites, based on the finding that urban yellow mongooses' home ranges are approximately 0.13 km^2 on average (Cronk and Pillay 2019a, 2021).

Experimental design and protocol

I used rectangular puzzle boxes made from clear Perspex, measuring 70 mm in height, 230 mm in length, and 150 mm in width (Figure 1).

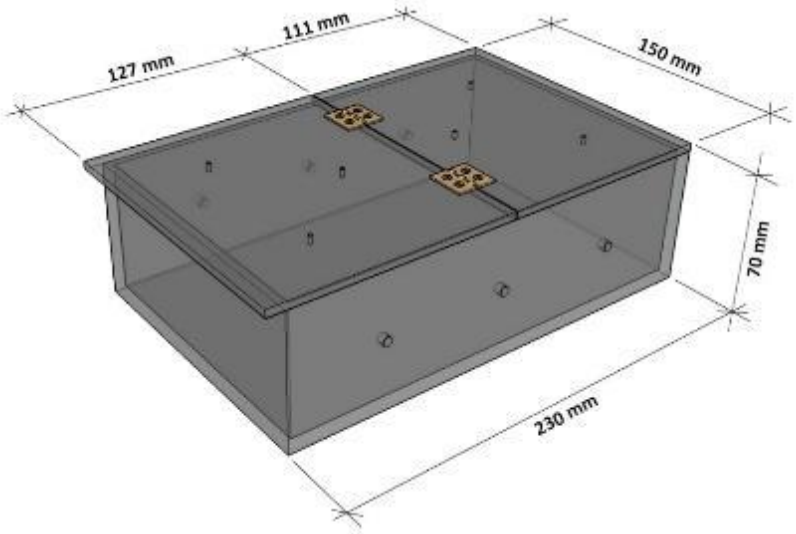


Figure 1. A diagram of a puzzle box used in a problem-solving study on yellow mongooses. The puzzle boxes were made of transparent Perspex, allowing mongooses to visually detect food incentives. Small holes were present in the lid and sides of the box to allow mongooses to detect food incentives by smell. The boxes could be opened or closed because of two metal hinges.

The puzzle boxes were placed at the selected sites to allow the mongooses to become habituated to this novel object. Meat offcuts (measured by volume; one teaspoon) were placed inside the puzzle and served as an incentive to solve the puzzle problem. This experiment took place between May and September 2019. The experiment was consistently set up and reset by three experimenters. At the start of every trial (defined as a single instance in which a mongoose interacted with a puzzle box), the food incentive was placed inside the box. This was done in the morning (between 06h00 and 12h00 when mongooses were most active, as established by Cronk and Pillay, 2019a, 2020). Mongooses were frequently, but not always, present during the set-up and resetting of the experiment. After the initial set-up at one site was completed, the same experiment was set up at the other sites (i.e. the experiment was conducted at all sites simultaneously). The experiment was reset daily or every second day, minimising the time between trials, to ensure that the mongooses remained habituated to the puzzle boxes. Each site was visited twice per day (between 06h00 and 12h00) and reset if the mongooses had consumed the food during the previous trial. This allowed for a maximum of two trials per site per day. Resetting the experiment involved clearing out any leftover food from the puzzle boxes and replenishing the same boxes with fresh food incentives. The same puzzle boxes were used for the duration of the experiment at each site (unless the puzzle box

was destroyed by large herbivores or removed by human residents, in which case it was replaced by a new puzzle box).

The puzzle box experiments consisted of two phases, a training phase and a testing phase, each with two stages. The training phase allowed mongooses to become habituated to the puzzle box and the food incentive before the testing phase commenced, reducing the effects of neophobia on their ability to solve the problem. During the training phase, the puzzle box lids were left open (stage 1; open stage), allowing the mongooses easy access to the food. In the next stage, the lid of the puzzle box was propped open slightly using a stick to create a small (±10 mm) opening, which allowed the mongooses to open the lid to access the food within the box (stage 2; propped stage). During the testing phase, the puzzle box was closed entirely, and the mongooses faced the novel problem of having to open the puzzle box (stage 3; closed stage). In the last stage, the puzzle box was closed entirely, and an object (a small bag of gravel wrapped in hessian) was placed on top of the lid, with a string attached to the object and the bottom of the puzzle box (stage 4; impediment stage; Figure 2). The object had a constant weight of 200 g (20% that of the average body weight of an adult yellow mongoose). The object served as an impediment which the mongooses had to remove from the top of the lid to open the puzzle box and obtain the food incentive. The string kept the lid closed when the mongooses lifted the lid with the object on top of the lid.

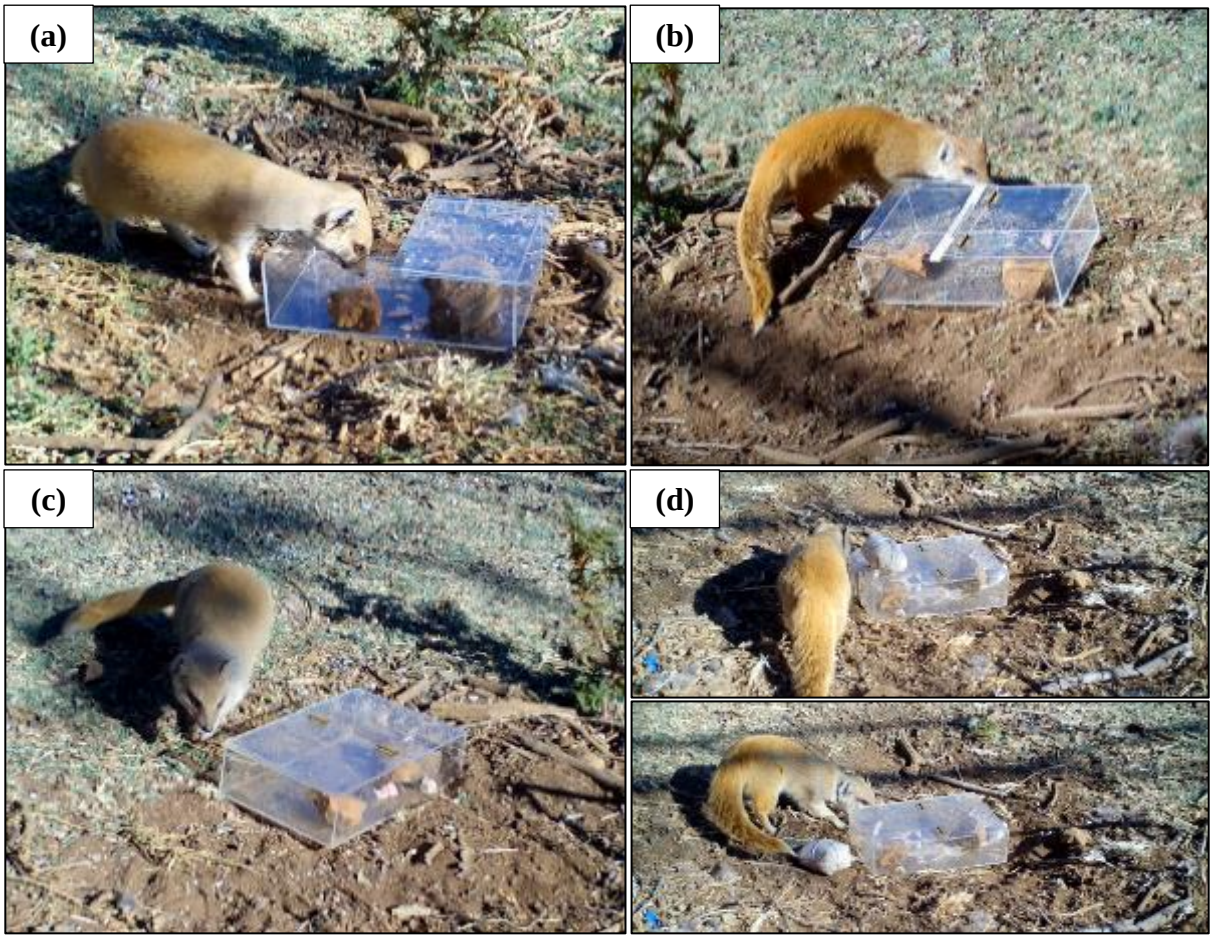


Figure 2. Puzzle box experimental set-up of **(a)** stage 1, open stage; **(b)** stage 2, propped stage; **(c)** stage 3, closed stage; and **(d)** stage 4, impediment stage. Boxes were weighed down with rocks from the immediate environment to prevent the boxes from being moved away from the site by wind or animals.

Because yellow mongooses are predominantly solitary foragers (le Roux et al., 2008; Manser et al., 2014), the same (focal) mongoose consistently visited the puzzle box experiments at each site (90% of all trials), but sometimes two or three mongooses were present at the puzzle box at once. Only adult mongooses participated in this study, as youngsters never attempted to solve the puzzle box problem. Further, males and females could not be distinguished due to the yellow mongoose's lack of sexual dimorphism, and therefore sex was not considered. Yellow mongooses have previously been trapped and collared in the Meyersdal estates, and, once trapped, never engaged with the trapping cage again (Cronk, personal communication). As a result of these negative trapping experiences for the mongooses in Meyersdal, permission for further trapping and marking was not obtained from the management, especially during the COVID-19 pandemic when veterinary assistance could not be provided. At the end of this study, facial recognition software was

developed with the assistance of the School of Computer Science and Applied Mathematics at the University of the Witwatersrand on high-quality photographs of the mongooses that participated in this study (obtained from camera trap footage). This software used several facial markers and machine learning to identify individual mongooses (unpublished data) to establish that the same individuals were continually interacting with the puzzle box at each site (likelihood models showed a high facial recognition accuracy of 90.2% with a confidence range of 88.1% to 97.3%).

Video analyses

Browning® Trail Cameras (Model BTC-8A; 55° field of view; Browning, 2019) triggered with a motion sensor were set up between 1 and 2 m away from the experiment with an unobstructed view of the puzzle box. Each trial started as soon as a mongoose entered the camera's field of view (1 – 2 m across) and ended as soon as the mongoose consumed the food incentive. From the camera trap footage, I recorded 1) the latency of the mongooses to investigate the puzzle box, 2) the duration that the mongooses took to complete the task, and 3) the interaction with the puzzle box. The latency to investigate the box was considered a measure of neophobia and was recorded as the number of seconds that elapsed from the moment an individual mongoose entered the field of view of the camera to its first contact with the puzzle box. The duration of completing the task was considered a measure of problem-solving ability and learning and was measured as the latency from first contact with the puzzle box to obtaining the food incentive. To provide a measure of behavioural persistence during their time of completing the task, the frequency of six interaction behaviours by the mongooses was scored, including (i) biting (clamping down on puzzle box with teeth), (ii) licking (contacting puzzle box with tongue), (iii) observing (body or head oriented towards the puzzle box but without making contact with the box), (iv) sniffing (nose touching the puzzle box without biting), (v) pawing (touching forepaw to sides or top of puzzle box or scratching at puzzle box without displacing it), and (vi) pushing/pulling (displacing the puzzle box away from or towards body using any body part). From this, behavioural diversity scores were generated for each trial as the number of behaviours performed during a given trial divided by the possible number of behaviours that could have been performed. This included the six behaviours as described above for stage 1 – 3, and an additional behaviour, nudging (nudging the lid of the box with muzzle in an upwards motion; attempt to lift the lid of the box with the impediment still in place), during stage 4. For

example, if a mongoose only performed 2 of the possible 6 behaviours during a trial in stage 1, the diversity score was 2/6 or 0.33, and if they performed 5 of the 7 possible behaviours during a trial in stage 4, the diversity score for that trial was 5/7 or 0.71. Thus, when fewer behaviours were performed, the behavioural diversity score was closer to 0, and when more behaviours were performed, the behavioural diversity score was closer to 1. Digging (the displacement of the ground underneath or next to the puzzle box using front paws) was also recorded but ultimately excluded from any analyses. This was due to uncertainty regarding the nature of this behaviour as digging sometimes appeared to resemble interaction with the box as mongooses attempted to access the food from underneath, and other times resembled frustration or possible displacement behaviour (the distinction between these two behaviours was not always clear).

I conducted this experiment at three sites initially and obtained a data set of 10 replicates (trials) for each stage. Using this initial dataset, I generated cumulative frequency graphs of the latency to consume the food incentive to determine the minimum number of trials taken to reach an asymptote. The graphs revealed an asymptote at five trials for stage 1, five trials for stage 2, six trials for stage 3, and nine trials for stage 4. I used these values to set the number of trials for all subsequent stages at the remaining sites.

Data analyses

All statistical analyses were conducted using R Statistical Software (R version 3.4.3; R Core Team, 2013; http://www.R-project.org/). Shapiro-Wilk tests were used to test for normality. Non-normal variables were transformed using a Box-Cox transformation (R package: MASS), and if variables could not be transformed, non-parametric tests were used. A linear mixed effect model (LMER; R packages: lme4, lmerTest) was used to analyse (i) the latency to consume the food (family = Gaussian; link = log). Generalised linear mixed models (GLMM) were used to analyse (ii) the latency to investigate the puzzle box (family = Gaussian; link = log), (iii) the frequency of behaviours (family = Poisson; link = log), and (iv) behavioural diversity scores (family = Gamma; link = log). The various stages were a repeated measures design, with stage and location as fixed effects, and site and trial as random factors. Tukey post hoc tests were used to determine pairwise differences for significant fixed factors (R packages: multcomp; lmerTest).

Ethical approval

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2017/03/19/B).

RESULTS

Problem-solving experiments were conducted on an urban population of yellow mongooses (n = 11) by providing them with puzzle boxes with four different stages of increasing complexity. Mongooses were able to solve the problem in each of the four stages, and thus had 100% success. Once the mongooses detected the food incentive inside the box, they often used interaction behaviours (e.g. biting, licking, observing, sniffing, pawing, and pushing/pulling) with the box (265 out of the 275 trials; 96%). These behaviours were consistent among the three locations. During stage 1 (open), the mongooses used interaction behaviours with the box during 47 of the 55 trials (85%), which always included sniffing the box. Because the lid was open, the mongooses were able to obtain the food incentive without physically interacting with the puzzle box. During stages 2 (propped) and 3 (closed), the mongooses started physically interacting with the box and displayed behaviours such as pawing at the lid of the box, biting and licking the box, and pushing and pulling the box. During stage 2, the mongooses used interaction behaviours with the puzzle box during 54 of the 55 trials (98%). The mongooses were able to open the box by finding the opening where the lid was propped up and lifting the lid by either inserting their muzzles into the opening and lifting the lid, or by biting the lid until the lid opened completely. Of the two techniques, lifting the lid with their snouts was the most used technique (occurring during > 80% of the trials). After the first few successful attempts at opening the box, the mongooses appeared to use the same technique for each consecutive trial and started to open the lids more effectively (indicated by a reduced solving latency). During stage 3, the mongooses had to locate the lid opening to guide them to where they could gain entrance to the food incentive. Because the lid extended over the edge of the box, the mongooses could lift the lid using their snouts even though the lid was closed. At this stage, the mongooses mostly used interaction behaviours with the puzzle box (62 out of the 66 trials; 94%) to find the lid through sniffing (61 out of the 62 trials; 98%). During stage 4 (impediment), the mongooses not only used interaction behaviours with the puzzle box but also with the impediment on top of the box. The mongooses always interacted with the box (99 out of the 99 trials; 100%). During 56 of the 99 trials (57%), the mongooses attempted to lift the lid without removing the impediment

first. These attempts were always unsuccessful since it was not possible to access the food without removing the object first. Although the impediment was sometimes knocked off the lid accidentally by the mongooses when interacting with the box, most trials consisted of the mongooses deliberately removing the impediment from the lid of the box (> 60% of trials) by pushing, biting, or pawing at the object until it fell off the box. After removing the impediment from the lid of the box, mongooses located and opened the box. After a few trials, the mongooses consistently used the same technique to remove the impediment from the lid (either pushing, biting, or swiping it off in a sideways movement with the front paws).

Latency to investigate

Location (χ^2 = 16.95, df = 2, p < 0.001; GLMM) and stage (χ^2 = 47.09, df =3, p < 0.001) were significant predictors of the latency to investigate the puzzle box (Figure 3). The interaction between location and stage was not a significant predictor of the latency to investigate the puzzle box (χ^2 = 4.89, df = 6, p = 0.557). Post-hoc tests showed that the latency to investigate the puzzle box was significantly longer in the Eco Estate compared with the Nature Estate (z = -3.63, p < 0.001), but the latency to investigate the puzzle box in the Retirement Home did not differ significantly from the Eco Estate or Nature Estate (Figure 3a). The latency to investigate the puzzle box was significantly longer in stage 1 compared with all other stages (stage 2: z = -4.46, p < 0.001; stage 3: -4.69, p < 0.001; stage 4: -5.43, p < 0.001; Figure 3b).

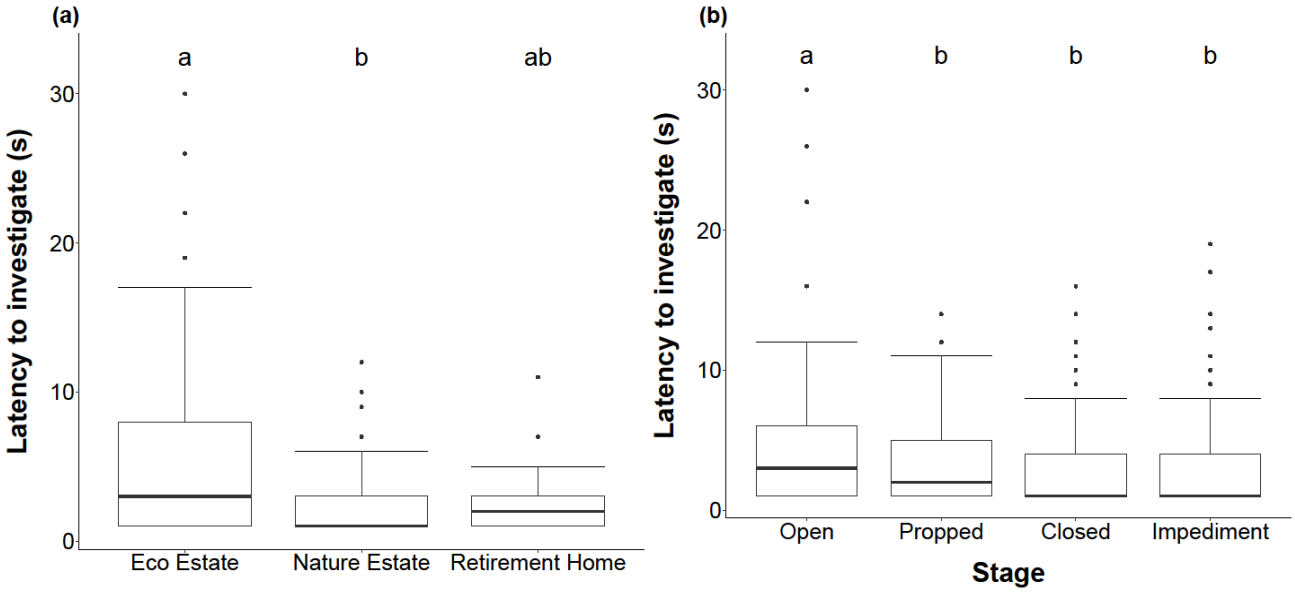


Figure 3. The latency to investigate (s) the puzzle box at **(a)** the Meyersdal Eco Estate, Meyersdal Nature Estate, and Renaissance Retirement Home and **(b)** four different stages with increasing levels of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between the three locations or the four stages.

Latency to consume

Location (χ^2 = 9.12, df = 2, p = 0.010; LMER) and stage (χ^2 = 185.77, df = 3, p < 0.001) were significant predictors of the latency to consume the food incentive (Figure 4). The interaction between location and stage was not a significant predictor of the latency to consume the food incentive (χ^2 = 3.13, df = 6 p = 0.079). Post hoc tests showed that the latency to consume the food incentive was the longest at the Eco estate, which was significantly longer than at the Retirement Home (t = 2.56, df = 11.3, p = 0.026; Figure 4a). The latency to consume the food incentive was significantly shorter in stage 1 compared with the other stages. The latency to consume was the longest during stage 4**,** differing significantly from stage 1 and stage 3 (t = -3.63, df = 88.1, p < 0.001; Figure 4b).

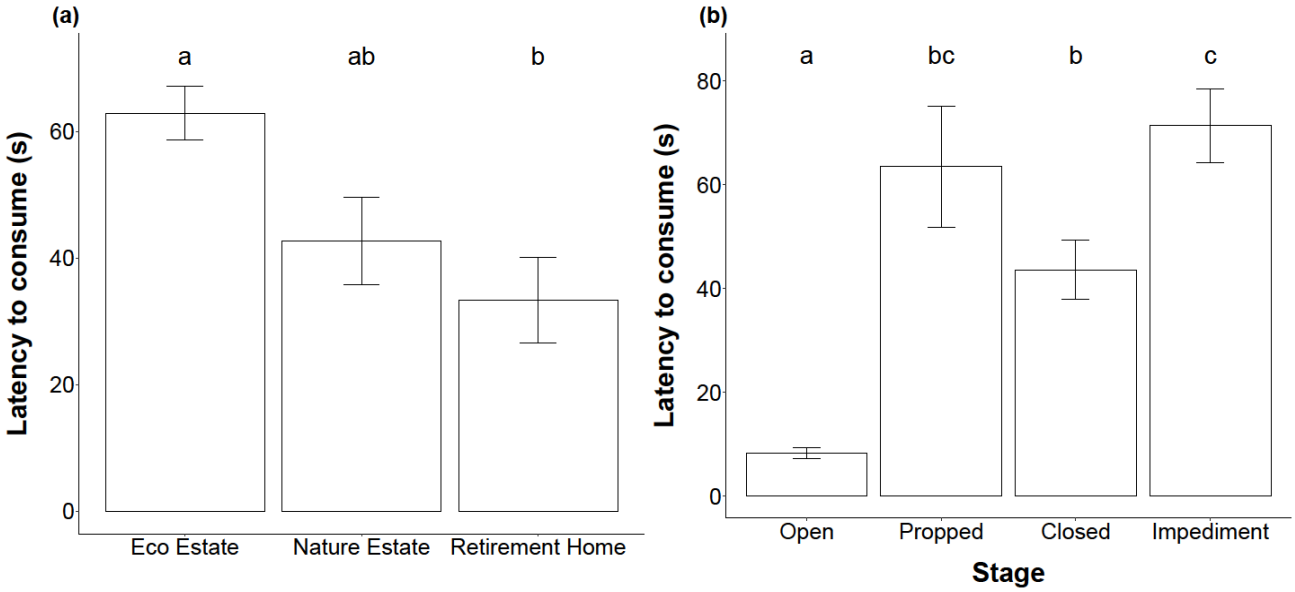


Figure 4. The mean latency to consume (s) the food incentive during puzzle box experiments at **(a)** the Meyersdal Eco Estate, Meyersdal Nature Estate, and Renaissance Retirement Home and **(b)** four different stages with increasing level of complexity. Error bars indicate standard error. The same alphabet letters indicate no significant difference between the three locations or four stages.

The latency to consume the food incentive differed with location and stage over the various trials. There was a general decrease in the latency to consume at each location, particularly during stage 2 in the Retirement Home, stage 3 in the Eco Estate and the Nature Estate, and stage 4 at all three locations (Figure 5).

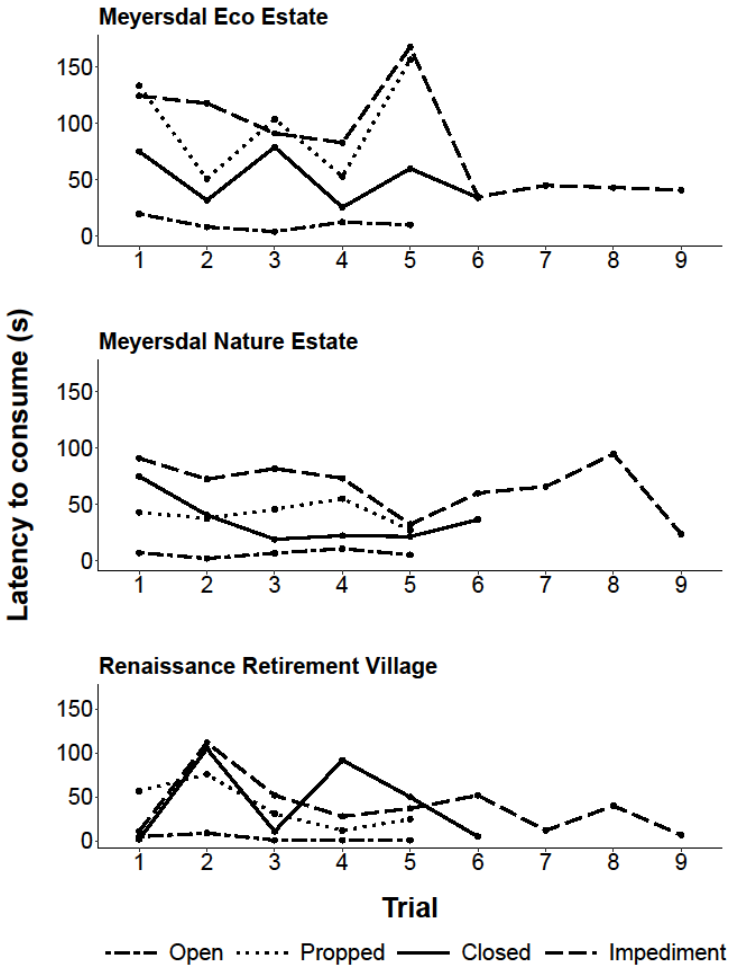


Figure 5. The mean latency to consume (s) the food incentive over the various trials when solving a puzzle box problem with four stages of increasing complexity at the three different locations.

Interaction behaviour

Stage was a significant predictor of the frequency of interaction with the puzzle box ($\chi^2 = 52.99$, df = 3, $p < 0.001$; GLMM; Figure 6). Location ($\chi^2 = 2.15$, df = 2, $p = 0.342$) and the interaction between location and stage ($\chi^2 = 3.18$, df = 6, $p = 0.786$) were not significant predictors of the frequency of interacting with the puzzle box. The frequency of interaction with the puzzle box at stage 1 was significantly lower than all other stages (stage 2: $z = 6.56$, $p < 0.001$; stage 3: $z = 4.92$, $p < 0.001$; stage 4: $z = 6.64$, $p < 0.001$). Although the frequency of interaction with the box was slightly higher at stage 3, it was still significantly lower than both stage 2 ($z = -2.89$, $p = 0.02$) and stage 4 ($z = 3.11$, $p = 0.001$; Figure 6).

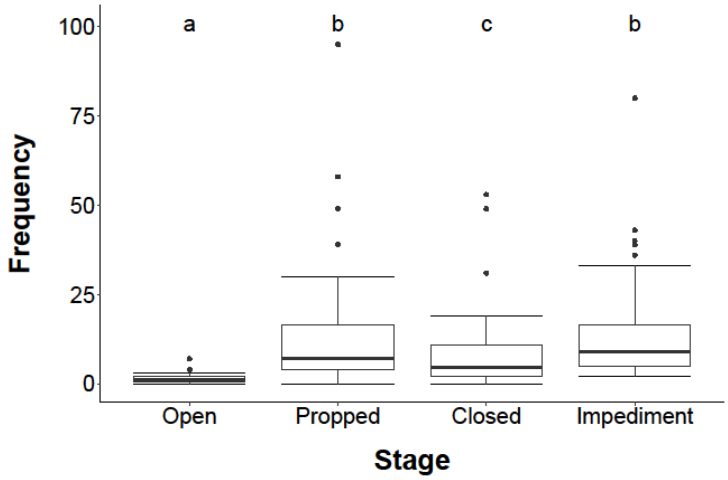


Figure 6. The frequency of interaction with the puzzle box before consuming the food incentive at four different stages with increasing level of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between the stages.

The frequency of interaction with the puzzle box remained relatively constant during stage 1 (open) but fluctuated over the various trials at stage 2 (propped), stage 3 (closed), and stage 4 (impediment). Even with this fluctuation, the overall frequency of interaction with the puzzle box decreased over the various trials (Figure 7).

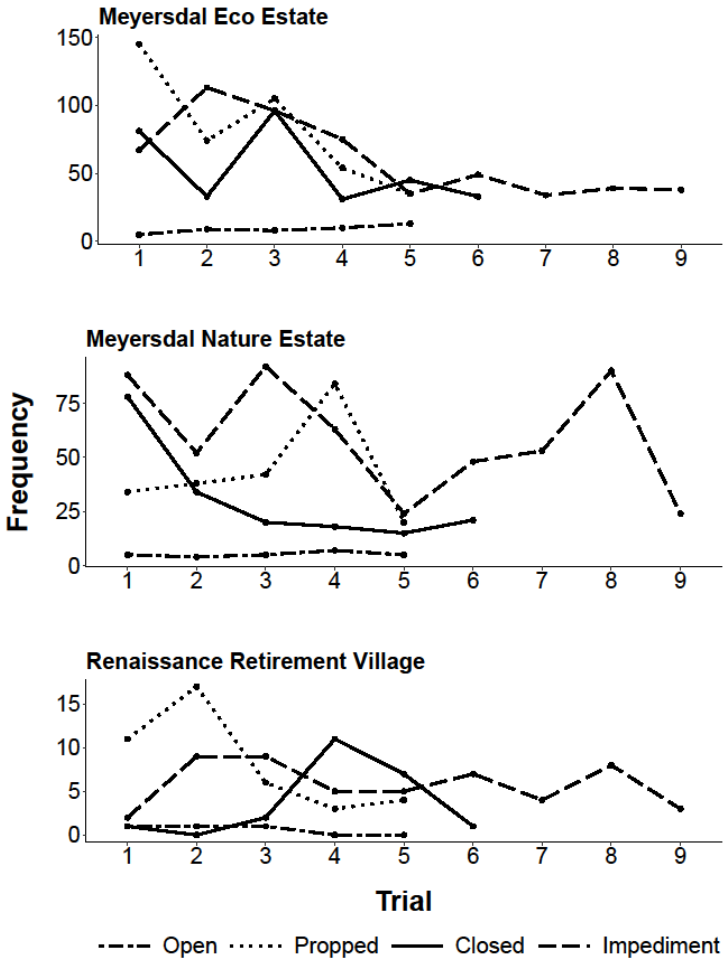


Figure 7. The frequency of interaction with the puzzle box over the various trials when solving a puzzle box problem with four stages of increasing complexity at the three different locations.

Stage was a significant predictor of behavioural diversity when interacting with the puzzle box ($\chi^2 = 60.41$, df = 3, $p < 0.001$; GLMM; Figure 8). Location ($\chi^2 = 4.59$, df = 2, $p = 0.101$) and the interaction between location and stage ($\chi^2 = 7.25$, df = 6, $p = 0.299$) were not significant predictors of the behavioural diversity displayed. The behavioural diversity score at stage 1 was significantly lower than all other stages (stage 2: $z = 7.92$, $p < 0.001$; stage 3: $z = 5.56$, $p < 0.001$; stage 4: $z = 10.14$, $p < 0.001$). Although the behavioural diversity score was slightly higher at stage 3, it was still significantly lower than both stage 2 ($z = -2.75$, $p = 0.030$) and stage 4 ($z = 4.50$, $p < 0.001$; Figure 8).

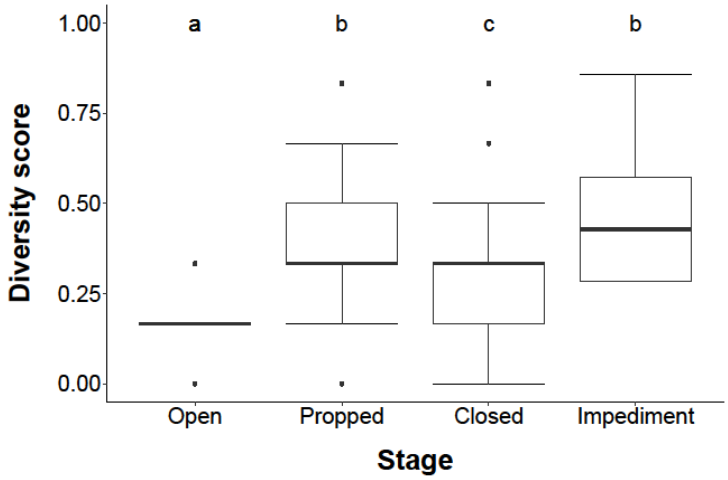


Figure 8. The behavioural diversity scores during interaction with the puzzles box before consuming the food incentive at four different stages with increasing level of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between the stages.

The behavioural diversity score varied over trials for each stage of difficulty at each location and never surpassed a score of 0.6 (Figure 9). There was a general decrease in the diversity score, especially at stage 3 (closed) and stage 4 (impediment), whereas the diversity scores remained relatively constant at stage 1 (open) and stage 2 (propped).

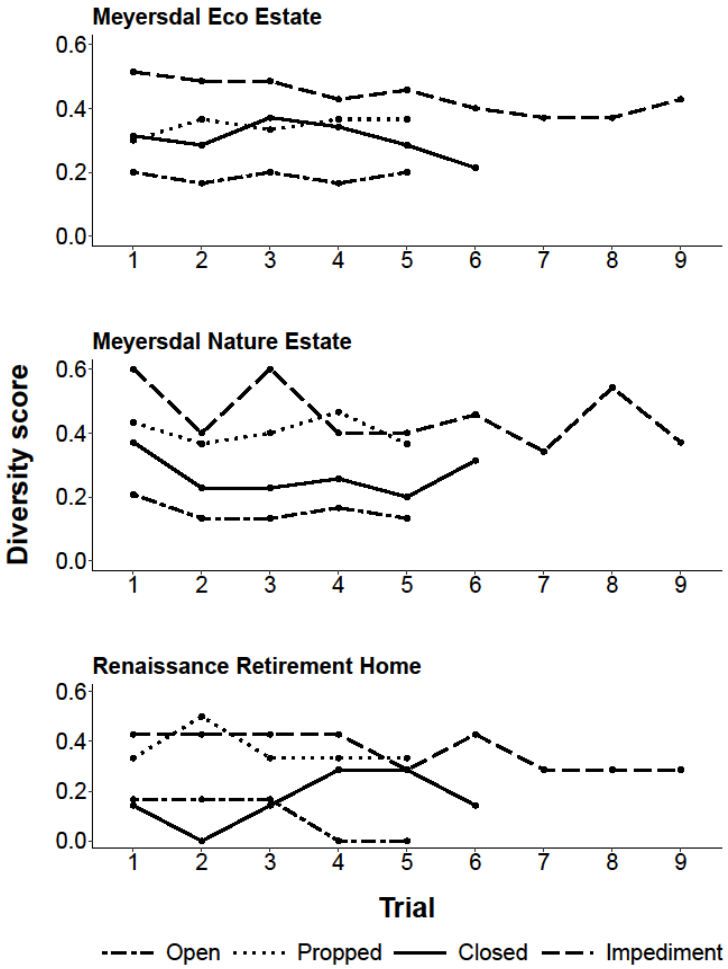


Figure 9. The behavioural diversity scores during interaction with the puzzle box over the various trials when solving a puzzle box problem with four stages of increasing complexity at the three different locations.

DISCUSSION

A puzzle box task experiment was conducted to assess whether yellow mongooses residing in an urban area were capable of learning to solve a novel problem with increasing levels of complexity. The yellow mongooses in three locations with differing levels of human contact showed the ability to solve a puzzle box problem at every stage of complexity. Those occurring in pockets of the built-up Meyersdal Eco Estate residential area took the longest time to solve the problem, whereas those frequently visiting a residential garden and home in the Glenvista Renaissance Retirement Village solved the problem the fastest. Furthermore, the mongooses were the quickest at accessing the food incentive during the first stage of complexity, but their duration of completing the task increased with the difficulty of the task at the subsequent stages of complexity. The duration of completing the task decreased over the various trials for each stage, potentially indicating learning. When attempting to solve the

problem, mongooses used a range of interactions (e.g. biting, licking, observing, sniffing, pawing, pushing/pulling, and nudging). The frequency at which these interaction behaviours were displayed (a measure of persistence), as well as the behavioural diversity scores (a measure of exploration), followed a similar pattern as the duration of completing the task and increased with the complexity of the task, especially at the second and fourth stages. Overall, the location of the mongoose colonies and the stage of complexity of the task were the main correlates of the mongooses' ability to successfully solve the problem faster over consecutive trials.

The mongooses occurring in the Nature Area were able to solve the puzzle box problem at every stage of complexity, most likely through innovation (the use of a novel behaviour to solve a problem; Reader and Laland, 2003). The ability to innovate and problem-solve is influenced by several factors, one of which is neophobia (Webster and Lefebvre, 2001; Greenberg, 2003; Benson-Amram and Holekamp, 2012). Those that are more neophobic are less likely to successfully solve a problem, as the fear of novelty must first be overcome before innovation can take place. The mongooses exhibited an initial neophobic response to the puzzle box during stage 1 (open), but this decreased significantly in the subsequent stages, where the mongooses had already become habituated. The mongooses in the Eco Estate had a stronger neophobic response than those in the Nature Estate and approached the puzzle boxes significantly slower. Because mongooses in the Eco Estate came into regular contact with human residents and other disturbances, such as motor vehicles, domestic animals, noise created by lawnmowers, construction, and so on, compared with those in the Nature Estate, which did not encounter such disturbances often, it is possible that the increased disturbance contributed to a heightened neophobic response. Although mongooses in the Eco Estate had an initial neophobic response, the mongooses here did also eventually become habituated to the puzzle box in the subsequent stages, as indicated by the decreased latency to investigate over the various stages.

The mongooses in the Eco Estate took the longest to solve the problem during each trial, and the mongooses were able to solve the problem the fastest in the Retirement Home. Since the latency to investigate, which was used as a metric for neophobia, did not differ between these two locations, it is unlikely that mongooses' problem-solving success was influenced by their neophobic response. These results are in contrast to many studies where problem-solving ability is influenced by neophobia. For example, less neophobic spotted hyaenas were more successful at problem-solving than more neophobic individuals (Benson-Amram and Holekamp, 2012), less neophobic raccoons were more likely to find innovative

solutions to a puzzle box task (Daniels et al., 2019), and neophobia was negatively correlated with innovative ability in Carib grackle, *Quiscalus lugubris* (Overington et al., 2011). Other than neophobia, there were three major differences observed among the locations that may have contributed to their problem-solving success (though neither one of these were measured directly): levels of tameness (i.e. habitation to the presence of humans), levels of disturbance (i.e. presence of humans, vehicular traffic, construction, noise, etc.), and food availability (i.e. accessibility and abundance).

The mongooses in the Retirement Home were the tamest, often entering people's homes searching for food, and those in the Eco Estate were the least tame and were almost always out of sight during the setting up of the puzzle box experiments (pers. obs.). Some studies have found a positive correlation between the level of habituation to humans and innovation (e.g. tamer feral pigeons, *Columba livia*, are faster at learning to access the food than the less tame zenaida doves, *Zenaida aurita*; Seferta et al., 2001). Still, other studies have found no correlations or even negative correlations (e.g. great tits, *Parus major*, Cole et al., 2011; Carib grackle, Overington et al., 2011; zenaida doves, Boogert et al., 2010), indicating that the relationship between flexible behaviours (such as innovation) and urbanisation, is complex and dynamic (Papp et al., 2015), and that this relationship should be investigated further (Overington et al., 2011).

The mongooses in the Retirement Home were fed by residents daily before this study was conducted. Thus, these individuals were likely well-fed and in good condition during the period of this study and could invest their time and energy into problem-solving ("spare time" hypothesis; Kummer and Goodall, 1985). Conversely, the mongooses in the Eco Estate may not have been as well fed, and moreover, regularly had to avoid disturbances such as hikers, motor vehicles, stray pets, and noise, prohibiting them from devoting time and energy to problem-solving. Having spare time and ample energy appears to be a consistent predictor of problem-solving ability. This is especially apparent in younger individuals that are known to be more explorative and innovative than older individuals (e.g. Biondi et al., 2010; Thornton and Samson, 2012), possibly because these individuals are cared for by older individuals and they thus have more time to explore and innovate (Kummer and Goodall, 1985).

One apparent problem with the "spare time" hypothesis is that it does not consider the role of motivation. Well-fed animals may not have internal cues, such as hunger, which contribute to the motivation to solve a complex puzzle to obtain food if it is already in a positive energy balance. For example, Laland and Reader (1999) showed that the most innovative guppies, *Poecilia reticulata*, were those that were deprived of food. Similarly,

subdominant (juvenile) blue tits, *Cyanistes caeruleus*, and great tits were better problem-solvers than their dominant adult counterparts (Morand-Ferron et al., 2011). These studies support the "necessity" hypothesis, which suggests that innovative predispositions are related to the ability to outcompete others for resources, since those who are unable to outcompete others for food would have to find alternative ways of obtaining nutrition and often do so through innovation (Reader and Laland, 2003). Results from studies testing this hypothesis, however, are inconsistent (Reader et al., 2016). In a review of 19 studies considering the role of necessity in innovation, Griffin and Guez (2014) found 12 studies showing a positive correlation, the remainder showing no correlation. Thus, it is most likely that the differences in problem-solving among the three locations in my study are due to a surplus in time and energy, rather than a shortage thereof, in mongooses occurring in the Retirement Home (since these mongooses were fed by humans daily) compared with the Eco Estate. These conflicting hypotheses demonstrate that more research into animal innovations is necessary, especially in cooperative breeders where social hierarchies and competitive differences are evident (Thornton and Samson, 2012).

The mongooses successfully solved the puzzle box problem at every stage of complexity. They were the fastest at solving the problem during stage 1 (open) since they could access the food incentive from the open box without having to interact with the box for too long. The latency to consume spiked at stage 2 (propped) when the mongooses had to determine how to lift the lid of the puzzle box. It is possible that they were able to do so through simple trial-and-error learning, similar to that observed in meerkats (Thornton and Samson, 2012). After the mongooses had learned to open the puzzle box, they were able to open the lid faster during stage 3 (closed) than in stage 2. From stage 2 to stage 3, the mongooses only became more proficient at solving the problem and did not have to learn any new behaviours or interact with any new components of the puzzle box; they were able to use the knowledge acquired from the previous stage and use the same technique to lift the lid. Stage 4 (impediment) was the most complex since the mongooses had to perform two steps to open the box, and could not use the same technique as before, so the latency to consume the food incentive increased again. Using incremental steps, the mongooses ultimately showed the ability to solve a complex novel puzzle box problem involving four steps. Perhaps the introduction of these incremental steps played a significant part in the mongooses' ability to solve the problem at the most complex stage. This method of scaffold learning, which simplifies a novel task to a level at which an individual can solve the problem before

increasing the complexity, may have aided the mongooses in successfully learning to solve the puzzle box problem at all stages of complexity.

Scaffold learning is typically used by adults when facilitating learning in their offspring to acquire new skills via incremental steps (Luef and Liebal, 2012). Thus, it is possible that, since youngsters, in general, learn from adults through scaffold learning, adult mongooses can learn through a series of incremental steps. Scaffolding has been observed in various animal species (e.g. western lowland gorillas, *Gorilla gorilla gorilla*, Whiten, 1999; pigtail macaques, *Macaca nemestrina*, Maestripieri, 1996; chimpanzees, *Pan troglodytes*, Boesch, 1991, and domestic cats, *Felis catus*, Caro, 1980) and usually involved the learning of skills such as locomotion and foraging. If scaffold learning is typically used in mongooses where adults present challenges to youngsters through scaffolding, it is expected that the experimental set-up played to the mongooses' advantage by presenting them with a similar learning method. Though scaffold learning is often observed in youngsters, literature on this form of learning in adult animals is lacking. Importantly, adult mongooses are largely solitary foragers (le Roux et al., 2008; Manser et al., 2014) and learning to solve the problem generally occurred through individual learning. Furthermore, to my knowledge, no literature exploring scaffold learning in mongooses exists, though such experiments would be an interesting addition to the existing knowledge on mongooses' cognition. Lastly, there was a general decrease in the latency to consume over the various trials at all three locations and all four stages, indicating that the mongooses became more proficient at solving the puzzle box problem over time.

The frequency at which mongooses interacted with the puzzle box (indicative of behavioural persistence), as well as the behavioural diversity (indicative of levels of exploration), did not differ among the three locations. Thus, it was unlikely that persistence and exploration contributed to their problem-solving efficiency, since the speed at which mongooses learned to solve the problem did indeed differ among the locations. The frequency of interaction and behavioural diversity scores followed a similar pattern to the latency to consume the food incentive. Both were lowest at stage 1 because the mongooses did not have to interact with the puzzle box to gain access to the food incentive, followed by a spike at stage 2 as interaction with the box was required, a slight decrease at stage 3 because the increase in the level of complexity from the previous stage was not as marked, and another spike at stage 4, when the task involved not only lifting the lid but also removing the impediment from the lid of the box beforehand, increasing the complexity of the task and behaviours required to solve the problem.

The frequency and diversity of interaction with the puzzle box generally decreased over the various trials for each of the four stages of complexity. This indicates that the mongooses interacted with the box most initially at every stage of complexity, after which the frequency decreased overall, eventually resulting in the lowest frequency of interaction during the last trial of every stage of complexity. Three cognitive factors contribute to innovation: inhibitory control, instrumental learning of motor actions, and the ability to extract a general rule (Hauser, 2003; Thornton and Samson, 2012). Firstly, inhibitory control is the inhibition of behaviours that do not result in successfully solving the problem and is considered a form of learning that allows individuals to solve a problem faster. Thus, inhibitory control influences innovation positively (Reader et al., 2016). Most interaction behaviours performed by the mongooses in my study were unlikely to result in them opening the box. Sniffing, observing, pawing, and licking, were never used to open the puzzle box, although biting occasionally resulted in the lid of the box being opened. Thus, the mongooses often spent a substantial amount of time performing these behaviours at the puzzle box with no success. However, if they inhibited the urge to perform these "unnecessary" behaviours, they might have been able to access the food incentive considerably faster. Benson-Amram and Holekamp (2012) found that exploration diversity and persistence were the two major behavioural traits contributing to the success of solving a puzzle box problem. Persistence is an important contributor to problem-solving success (as seen in woodpecker finches, *Cactospiza pallida*, Tebbich et al., 2010; meerkats, Thornton and Samson, 2012; spotted hyaenas, Benson-Amram and Holekamp, 2012) since individuals that do not give up easily are more likely to solve the problem than those who do (Thornton and Samson, 2012). However, persistently performing behaviours that will not result in solving the problem will inevitably hinder problem-solving success (Hauser, 1999). In order to successfully solve a problem, individuals thus need to inhibit unnecessary behaviours and instead learn which behaviours will contribute to successfully solving the problem (Benson-Amram and Holekamp, 2012). The decrease in interaction frequency and diversity over the various trials suggest that mongooses are capable of inhibitory control.

Secondly, learning new motor actions necessary to successfully access the food incentive possibly played a role in the decrease in the frequency of interaction behaviours and behavioural diversity over the various trials. The design of the puzzle boxes in this study required the mongooses to use a novel behaviour and motor action to lift the lid of the puzzle box to access a food incentive. The upward motion of the head used by the mongooses to lift the lid with their snouts has not been observed when they forage for food in their natural

environment. Instead, digging in the ground and/or biting objects to obtain a food item is commonly observed (Cronk and Pillay, 2018). These behaviours were used at the puzzle boxes initially, and the novel, upward motion of the head to obtain food, was later learned. Thus, once they successfully solved the problem, they had to memorise and recall this previously novel behaviour during consecutive trials to gain access to the food incentive in subsequent trials. This could potentially explain why the mongooses showed lower frequencies of interaction and behavioural diversity during stage 3 compared with stage 2, because the mongooses had already learned how to perform this behaviour during stage 2. Thirdly, the mongooses showed the ability to extract a general rule (lift the lid to obtain the reward) and were able to apply this rule to the subsequent stages. No matter how the box was oriented, whether the lid was propped up or the box was completely closed, or whether there was an impediment on the lid, the mongooses located and lifted the lid using the same technique to obtain the food incentive. Overall, mongooses appeared to utilise techniques typically associated with innovation in animals to solve the puzzle-box problem.

Urban-dwelling yellow mongooses in my study showed the ability to solve a novel feeding task. The mongooses' problem-solving efficiency differed among three locations with differing extents of human interaction. Their problem-solving ability did not correlate with the differing levels of neophobia among the three locations and could more likely be attributed to their individual levels of tameness or the varying degrees of disturbance among the locations, though this was not directly tested. Furthermore, the frequency of interaction with the puzzle box and the diversity of behaviours displayed when solving a problem may have aided mongooses in solving the puzzle box problem at more complex stages. However, these levels of persistence and exploration did not differ among locations and were, therefore, unlikely to be a predictor of problem-solving efficiency. The innovative ability of mammalian carnivores (order Carnivora) has been reported in numerous species (e.g. meerkats, Thornton and Samson, 2012; spotted hyaenas, Benson-Amram and Holekamp, 2012; bat-eared foxes, *Otocyon megalotis*, Jacobs, 2015; raccoons, Daniels et al., 2019), and now also in urban yellow mongooses. Furthermore, urban-living animals have been shown to be proficient in innovative problem-solving, which might be either a consequence or the cause of their successful invasion of urban areas. My study shows that urban-living yellow mongooses are not only capable of interacting with novelty in an anthropogenic environment, but also able to solve novel problems through innovation to obtain food. Further research is still needed to explore the mechanisms and extent of these animals' cognitive abilities.

REFERENCES

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature, 554*(7692), 364–367. doi: 10.1038/nature25503

Avenant, N. L., & Nel, J. A. J. (1992). Comparison of the diet of the yellow mongoose in a coastal and a Karoo area. *South African Journal of Wildlife Research*, *22*, 89–93.

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095. doi: 10.1098/rspb.2012.1450

Benson-Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour, 85*(2), 349–356. doi: 10.1016/j.anbehav.2012.11.003

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). *Animal Cognition*, *12*(1), 63–73. doi: 10.1007/s10071-008-0171-2

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal Cognition*, *13*(5), 701–710. doi: 10.1007/s10071-010-0319-8

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*(3), 530–532. doi: 10.1016/S0003-3472(05)80857-7

Boogert, Neeltje J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origin and spread of innovations in starlings. *Animal Behaviour*, *75*(4), 1509–1518. doi: 10.1016/j.anbehav.2007.09.033

Boogert, N. J., Monceau, K., & Lefebvre, L. (2010). A field test of behavioural flexibility in zenaida doves (*Zenaida aurita*). *Behavioural Processes*, *85*(2), 135–141. doi: 10.1016/j.beproc.2010.06.020

Bouchard, J., Goodyer, W., & Lefebvre, L. (2007). Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, *10*(2), 259–266. doi: 10.1007/s10071-006-0064-1

Browning. (2019). Browning Trail Cameras: Advantage SpecOps Full HD Video Model BTC-8A: Instruction Manual. Browning. Retrieved from https://browningtrailcameras.zendesk.com/hc/en-us/article_attachments/360073084653/Spec_Ops_Advantage_BTC-8A.pdf.

Caro, T. M. (1980). Predatory behaviour in domestic cat mothers. *Behaviour*, *74*(1–2), 128–147. doi: 10.1163/156853980X00357

Cavallini, P., & Nel, J. A. J. (1995). Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). *South African Journal of Zoology*, *30*(2), 46–49. doi: 10.1080/02541858.1995.11448371

Cole, E. F., Cram, D. L., & Quinn, J. L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. *Animal Behaviour*, *81*(2), 491–498. doi: 10.1016/j.anbehav.2010.11.025

Cronk, N. E., & Pillay, N. (2018). Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethologica*, *21*(2), 127–136. doi: 10.1007/s10211-018-0291-x

Cronk, N. E., & Pillay, N. (2019a). Flexible use of urban resources by the yellow mongoose *Cynictis penicillata*. *Animals*, *9*(7), 447. doi: 10.3390/ani9070447

Cronk, N. E., & Pillay, N. (2020). Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment. *Journal of Urban Ecology*, *6*(1), 1–9. doi: 10.1093/jue/juaa013

Cronk, N. E., & Pillay, N. (2021). Home range and use of residential gardens by yellow mongoose *Cynictis penicillata* in an urban environment. *Urban Ecosystems*, *24*(1), 127–139. doi: 10.1007/s11252-020-01022-1

Cronk, N., & Pillay, N. (2019b). Dietary overlap of two sympatric African mongoose species in an urban environment. *Mammalia*, *85*(5), 428–438. doi: 10.1515/mammalia-2018-0113

Daniels, S. E., Fanelli, R. E., Gilbert, A., & Benson-Amram, S. (2019). Behavioral flexibility of a generalist carnivore. *Animal Cognition*, *22*(3). doi: 10.1007/s10071-019-01252-7

Do Linh San, E., Cavallini, P., & Taylor, P. (2015). *The IUCN Red List of Threatened Species 2015* [Data set]. International Union for Conservation of Nature. doi: 10.2305/IUCN.UK.2015-4.RLTS.T41597A45205726.en

Dugatkin, L. A. (2004). *Principles of animal behavior*. New York: W.W. Norton & Company.

Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 347–374. doi: 10.1146/annurev.ecolsys.35.112202.130152

Gajdon, G. K., Fijn, N., & Huber, L. (2006). Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Animal Cognition*, *9*(3), 173–181. doi: 10.1007/s10071-006-0018-7

Greenberg, R. S. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In S. M. Reader & K. N. Laland (Eds.), *Animal innovation* (pp. 175–196). Oxford ; New York: Oxford University Press.

Hauser, M. D. (1999). Perseveration, inhibition and the prefrontal cortex: A new look. *Current Opinion in Neurobiology*, *9*(2), 214–222. doi: 10.1016/S0959-4388(99)80030-0

Hauser, M. D. (2003). To innovate or not to innovate? That is the question. In S. M. Reader & K. N. Laland (Eds.), *Animal innovation* (pp. 329–338). Oxford ; New York: Oxford University Press.

Huebner, F., & Fichtel, C. (2015). Innovation and behavioral flexibility in wild redfronted lemurs (*Eulemur rufifrons*). *Animal Cognition*, *18*(3), 777–787. doi: 10.1007/s10071-015-0844-6

Isabella, J. (2016, March 31). The intelligent life of the city raccoon. Retrieved March 29, 2019, from Nautilus website: http://nautil.us/issue/34/adaptation/the-intelligent-life-of-the-city-raccoon-rp

Jacobs, P., J. (2015). *Innovation and problem solving in bat eared foxes, Otocyon megalotis*. M. Sc. Thesis. University of the Free State, Bloemfontein.

Johnson-Ulrich, L., Johnson-Ulrich, Z., & Holekamp, K. (2018). Proactive behavior, but not inhibitory control, predicts repeated innovation by spotted hyenas tested with a multi-access box. *Animal Cognition*, *21*(3), 379–392. doi: 10.1007/s10071-018-1174-2

Kingdon, J., Happold, D., Butynski, T., Hoffman, M., Happold, M., & Kalina, J. (Eds.). (2013). *Cynictis penicillata*, Yellow Mongoose. In *Mammals of Africa. Vol. 5: Carnivores, pangolins, equids and rhinoceroses* (pp. 334–339). London: Bloomsbury.

Klump, B. C., Major, R. E., Farine, D. R., Martin, J. M., & Aplin, L. M. (2022). Is bin-opening in cockatoos leading to an innovation arms race with humans? *Current Biology, 32*(17), R910–R911. doi: 10.1016/j.cub.2022.08.008

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *308*(1135), 203–214. doi: 10.1098/rstb.1985.0020

Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour, 57*(2), 331–340. doi: 10.1006/anbe.1998.0967

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behaviour*, *75*(3), 943–949. doi: 10.1016/j.anbehav.2007.07.014

Luef, E. M., & Liebal, K. (2012). Infant-directed communication in lowland gorillas (*Gorilla gorilla*): Do older animals scaffold communicative competence in infants? *American Journal of Primatology*, *74*(9), 841–852. doi: 10.1002/ajp.22039

Maestripieri, D. (1996). Maternal encouragement of infant locomotion in pigtail macaques, *Macaca nemestrina*. *Animal Behaviour, 51*(3), 603–610. doi: 10.1006/anbe.1996.0064

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal Complexity in Meerkats and Other Mongoose Species. *Advances in the Study of Behavior*, *46*, 281–310. doi: 10.1016/B978-0-12-800286-5.00006-7

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience, 52*(10), 883–890. doi: 10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. doi: 10.1016/j.biocon.2005.09.005

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: Associative learning in wild great tits. *PLOS ONE, 10*(8), e0133821. doi: 10.1371/journal.pone.0133821

Morand-Ferron, J., Cole, E. F., Rawles, J. E. C., & Quinn, J. L. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology, 22*(6), 1241–1248. doi: 10.1093/beheco/arr120

Nel, J. A. J., & Kok, O. B. (1999). Diet and foraging group size in the yellow mongoose: A comparison with the suricate and the bat-eared fox. *Ethology Ecology & Evolution*, *11*(1), 25–34. doi: 10.1080/08927014.1999.9522839

Ngalo, S. (2014). Yellow mongoose—SANBI. Retrieved March 28, 2018, from https://www.sanbi.org/animal-of-the-week/yellow-mongoose/

Overington, S. E., Cauchard, L., Côté, K.-A., & Lefebvre, L. (2011). Innovative foraging behaviour in birds: What characterizes an innovator? *Behavioural Processes*, *87*(3), 274–285. doi: 10.1016/j.beproc.2011.06.002

Papp, S., Vincze, E., Preiszner, B., Liker, A., & Bókony, V. (2015). A comparison of problem-solving success between urban and rural house sparrows. *Behavioral Ecology and Sociobiology*, *69*(3), 471–480. doi: 10.1007/s00265-014-1859-8

Prasher, S., Evans, J. C., Thompson, M. J., & Morand-Ferron, J. (2019). Characterizing innovators: Ecological and individual predictors of problem-solving performance. *PLOS ONE*, *14*(6), e0217464. doi: 10.1371/journal.pone.0217464

Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., & Healy, S. D. (2016). Why study cognition in the wild (and how to test it)? *Journal of the Experimental Analysis of Behavior*, *105*(1), 41–55. doi: 10.1002/jeab.195

Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, *30*(04), 393 –437. doi: 10.1017/S0140525X07002373

R Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reader, S. M., & Laland, K. N. (2003). Animal Innovation: An Introduction. In S. M. Reader & K. N. Laland (Eds.), *Animal Innovation* (pp. 3–36). Oxford University Press. doi: 10.1093/acprof:oso/9780198526223.003.0001

Reader, S. M., Morand-Ferron, J., & Flynn, E. (2016). Animal and human innovation: Novel problems and novel solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150182. doi: 10.1098/rstb.2015.0182

Seferta, A., Guay, P.-J., Marzinotto, E., & Lefebvre, L. (2001). Learning differences between feral pigeons and zenaida doves: The role of neophobia and human proximity. *Ethology*, *107*, 281–293. doi: 10.1046/j.1439-0310.2001.00658.x

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Tebbich, S., Sterelny, K., & Teschke, I. (2010). The tale of the finch: Adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1543), 1099–1109. doi: 10.1098/rstb.2009.0291

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468. doi: 10.1016/j.anbehav.2012.03.018

Webster, S. J., & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, *62*(1), 23–32. doi: 10.1006/anbe.2000.1725

Whiten, A. (1999). Parental encouragement in gorilla in comparative perspective: Implications for social cognition and the evolution of teaching. In S. T. Parker, S. T. Parker, R. W. Mitchell, & H. L. Miles, *The mentalities of gorillas and orangutans: comparative perspectives* (pp. 342–366). Cambridge, U.K.: Cambridge University Press.

CHAPTER 3

Cognitive flexibility in urban yellow mongoose, *Cynictis penicillata*



ABSTRACT

Cognitive flexibility allows animals to alter their behaviour and respond appropriately to environmental changes. Importantly, once previously learned behavioural responses become inappropriate in an alternate setting, learning new appropriate responses is beneficial to achieve the desired behavioural outcome continually. Such flexibility is especially important in urban settings where environmental changes occur rapidly and continuously. I have previously shown that urban-dwelling yellow mongooses, *Cynictis penicillata*, in South Africa can learn to solve a puzzle box problem of increasing complexity. However, whether they are cognitively flexible and can adjust their behaviour based on environmental changes is unknown. To assess yellow mongooses' cognitive flexibility, I conducted two experiments: reversal learning and attention task. Reversal learning experiments were conducted using two puzzle boxes with distinct visual and spatial discrimination, each containing a preferred (meat) or non-preferred (bread) food type. Once mongooses learned which box contained the preferred food type, the food types were reversed between the two boxes. The mongooses successfully unlearned their previously learned response in favour of learning a new, appropriate response to continually access the preferred food, possibly through a win-stay, lose-shift strategy. Attention task experiments were conducted using one puzzle box surrounded by zero, one, two, or three objects providing various levels of distraction while solving the puzzle box problem. This design allowed me to assess whether mongooses could use divided attention to solve the problem whilst remaining vigilant to the distractions. Mongooses were able to solve the puzzle box problem in the face of distraction, but it would take mongooses on average twice as long to solve the problem during the most distraction than no distraction. Still, the mongooses managed to split their attention between the puzzle box problem and remaining vigilant to high levels of distractions. These results provide evidence of cognitive flexibility in urban yellow mongooses, enabling them to adapt their behaviour to changes in environmental stimuli.
Keywords: *attention; flexibility; problem-solving; reversal learning; urban; yellow mongoose*

INTRODUCTION

The ability of animals to continually learn and alter goal-directed behaviour, even as the learning contingencies change, demonstrates cognitive flexibility (Klanker et al., 2013; Tello-Ramos et al., 2019). Cognitive flexibility enables animals to adapt to rapidly changing environments (Sol, 2009), particularly in generalist species that frequently respond to

environmental variability (Mettke-Hofmann, 2014; Sol et al., 2016). However, not all species have comparable levels of cognitive flexibility. For example, Gonzalez et al. (1967) found that pigeons, *Columbia livia*, were cognitively more flexible than goldfish, *Carassius auratus*, when given the same reversal learning task. Interestingly, their cognitive flexibility appeared to be correlated with their memory retention abilities, with goldfish retaining the learned information, and pigeons' retention score decreasing over successive trials. This apparent trade-off between cognitive flexibility and memory retention has also been observed in black-capped chickadees, *Poecile atricapillus*, versus dark-eyed juncos, *Junco hyemalis* (Hampton et al., 1998), as well as mountain chickadees, *Poecile gambeli*, occurring at high versus low elevations (Freas et al., 2012; Tello-Ramos et al., 2018, 2019). This cognitive flexibility and memory retention trade-off, as well as interspecific variation in levels of cognitive flexibility (Lefebvre et al., 2004), might indicate potential costs associated with being cognitively flexible (Tello-Ramos et al., 2018). This means that different environments must favour either high levels of cognitive flexibility or greater memory retention (Tello-Ramos et al., 2018). As a result, cognitive flexibility should be retained in rapidly changing environments (Tello-Ramos et al., 2018), allowing animals to behave flexibly and adapt to urban environments (Sol et al., 2013).

Reversal learning

Learning is an essential aspect of behavioural flexibility, enabling animals to alter their behaviour based on their previous experiences (Lucon-Xiccato and Bisazza, 2014). However, in rapidly changing environments, it may be beneficial for individuals to inhibit their previously learned responses in order to perform a more appropriate behaviour (Lucon-Xiccato and Bisazza, 2014). This is known as reversal learning, and is an integral part of behavioural and cognitive flexibility (Lucon-Xiccato and Bisazza, 2014; Liu et al., 2016; Izquierdo et al., 2017).

Reversal learning is customarily assessed by training an animal to distinguish between two stimuli, typically using a food incentive. Once the animal successfully discriminates between the stimuli, the outcome of the reward is reversed, and the animal must inhibit the previously learned response to continually obtain the reward (Lucon-Xiccato and Bisazza, 2014). Two methods of learning are utilised by animals when presented with a reversal learning task: associative learning followed by reversal learning. Associative learning involves an animal adjusting its behaviour with the use of reinforcement based on specific

associations between multiple stimuli or between stimuli and their outcomes (Ginsburg and Jablonka, 2010). This is considered a conserved form of learning since all bilaterally symmetrical animals can learn simple associations (Papini, 2002; Ginsburg and Jablonka, 2010; Bennett, 2021). Conversely, reversal learning involves unlearning the association formed during the associative learning phase and replacing it with a new association, which requires individuals to behave flexibly. But solving such a reversal learning task is more complex than the initial association. For example, female guppies, *Poecilia reticulata*, with larger brains, were no better at completing a simple associative learning task than those with smaller brains (Buechel et al., 2018). Still, they performed better at reversal learning tasks (Buechel et al., 2018). This indicates that individuals with larger brain sizes, a proxy for cognitive ability, are more likely to be cognitively flexible and can solve more complex tasks such as reversal learning. In contrast, simple associative learning tasks can be performed efficiently even by those with smaller brains (Buechel et al., 2018). Furthermore, individuals that solve reversal tasks more efficiently are more flexible than those that consistently make errors (Bond et al., 2007).

Performance on reversal learning tasks may be negatively correlated with performance on the initial associative learning task (Bebus et al., 2016). In other words, there appears to be a trade-off between initial associative learning and later reversal learning task performance, where individuals that perform better at the associative learning tasks perform worse at the reversal learning tasks (Bebus et al., 2016). This observation has been attributed to memory, with those individuals with better memories likely being less flexible due to forgetting more recently learned information (referred to as proactive interference), whereas those that are more forgetful may be more flexible since they remember recently learned information at the expense of forgetting previously learned information (referred to as retroactive interference; Croston et al., 2016). Proactive interference is considered a lower-order process (since the learning occurs involuntarily). It is, therefore, thought to represent a lower level of flexibility, especially when compared with rule-based strategies (e.g. win-stay, lose-shift), which represents a greater level of flexibility (Mackintosh et al., 1968; Parker et al., 2012; Liu et al., 2016). For example, mountain chickadees, *Poecile gambler*, that performed worse at a reversal learning task did so because they visited previously rewarded locations more frequently than recently rewarded locations, thus demonstrating proactive interference (Croston et al., 2016).

Various species show the ability to inhibit their previously rewarded response through reversal learning, including reptiles (e.g. rough-necked monitors, *Varanus*

rudicollis, Gaalema, 2011; *Anolis evermanni*, Leal and Powell, 2012; tree skinks, *Egernia striolata,* Szabo et al., 2018), fish (e.g. zebrafish, *Danio rerio*, Parker et al., 2012; guppies, Lucon-Xiccato and Bisazza, 2014), amphibians (poison frog, *Dendrobates auratus*, Liu et al., 2016), and mammals (e.g. domestic kittens, *Felis catus*, Warren and Warren, 1967; raccoons, *Procyon lotor*; striped skunks, *Mephitis mephitis*; coyotes, *Canis latrans*, Stanton et al., 2021). In addition, some animals have shown the ability to repeatedly change their behaviour through a series of reversals (serial reversal learning; e.g., Liu et al., 2016). The ability to perform such reversal learning tasks has been attributed to various internal factors (e.g. brain size, Buechel et al., 2017; memory, Croston et al., 2016), but more recently, it has been suggested that several social and ecological factors may further influence an animal's level of flexibility, and thus, reversal learning abilities. For example, social species of birds are better at performing reversal learning tasks than less social species (Bond et al., 2007). Similarly, Buechel et al. (2017) argue that animals living in social groups are expected to be highly flexible to cope with the demands of heightened social interactions. Furthermore, woodpecker finches, *Cactospiza pallida*, in variable environments are more flexible than those occurring in stable habitats (Tebbich and Teschke, 2014), and mountain chickadees from varying elevations show significant differences in reversal learning ability (Croston et al., 2016). This indicates that cognitive flexibility may be influenced by the immediate environment in which individuals occur, even within the same species or population. Additionally, urbanisation (Federspiel et al., 2017) and food availability (Tebbich and Teschke, 2014) are factors that predict whether or not reversal learning will be selected for. Stanton et al. (2021) assessed reversal learning in three urban generalist mesocarnivores (raccoons, striped skunks, and coyotes) and found that, although these species showed variability in their reversal learning abilities, they were all able to successfully solve reversal learning tasks. Similar studies on the yellow mongoose, *Cynictis penicillata*, a southern African urban generalist mesocarnivore, are lacking, however.

Divided attention

In an ideal world, animals would be able to interact with and solve problems without any distractions or interference. In this way, animals would be able to focus all their attention on the task at hand and devote 100% of their cognitive capacity to solving a problem. This is rarely the case in reality. Often, animals must pay as much, if not more, attention to their surroundings in an attempt to detect predators and avoid other dangers. Thus, animals are

more likely to divide their attention among many different tasks. This, however, is cognitively demanding (Griffiths et al., 2004; Zentall, 2005), and individuals may not always be capable of divided attention. Urban animals should have increased opportunities and time for problem-solving because they might not have the same levels of distraction, such as predator avoidance ("spare time" hypothesis; Kummer and Goodall, 1985), as their non-urban counterparts. However, urban animals are exposed to numerous other distractions, such as the presence of humans, vehicular traffic, noise, and so on, to which they must adapt. As a result, being cognitively flexible, and having the ability to switch between multiple cognitively demanding tasks, may further aid success in urban areas.

Attention refers to the selective way in which animals allocate their attention by processing certain stimuli and disregarding others. Selective attention is an animal's ability to focus on one task, process relevant information, and filter out unnecessary and irrelevant distractions in order to process and respond to the focal stimulus more efficiently (Zentall, 2005; Carlson et al., 2018). This allows animals to avoid cognitive overload or inappropriate behavioural responses while engaging in a task (Commodari, 2017). There are, however, costs associated with the use of selective attention. For example, blue-jays, *Cyanocitta cristata*, failed to notice an approaching predator while foraging due to their inability to divide their attention among various tasks (Dukas and Kamil, 2000). Conversely, divided attention is when an individual focuses on multiple tasks simultaneously and divides their attention equally among the tasks (Parasuraman, 1998). Although this type of attention may seem ideal when solving problems in the face of distractions, a possible shortfall when dividing attention is that the information may not be processed as efficiently, resulting in a decline in the performance of tasks, since processing two stimuli simultaneously is cognitively demanding (Griffiths et al., 2004; Zentall, 2005). For example, when blue-jays were presented with a task where they had to locate two prey items simultaneously, the detection rate was lower than when they only had to locate one prey item at a time (Dukas and Kamil, 2001). Similarly, Griffiths et al. (2004) tested the advantages of trout, *Salmo trutta*, associating with familiar individuals, and found a 14% increase in predator detection compared with those associating with unfamiliar individuals, possibly due to the distraction and demand for dividing attention that associating with unfamiliar individuals imposes.

An alternative mechanism of focusing on multiple stimuli is alternating attention, which involves rapidly shifting attention from one task to another, instead of focusing on the tasks in parallel (Commodari, 2017). This allows animals to terminate focus on one task in favour of focusing on a second task, before terminating focus on the second task in favour of

focusing again on the first (Commodari, 2017). This rapid shifting of attention is attributed to the incapacity of animals to focus their attention on two tasks simultaneously (Parasuraman, 1998). Still, it enables animals to respond to stimuli in their environment as they appear. Similar to reversal learning, the dividing or shifting of attention to focus on multiple stimuli may be a measure of cognitive flexibility, which involves switching between tasks as their priorities change (Diamond, 2013). Therefore, although cognitively demanding, divided attention may be beneficial for urban living.

The yellow mongoose, *Cynictis penicillata*, is a small (tail and body length: ±300 mm; body weight: 500 – 1000g; Kingdon et al., 2013), generalist carnivore (Bizani, 2014) distributed throughout southern Africa (Do Linh San et al., 2015). It is adapted to urban environments where it consumes anthropogenic food items (Cronk and Pillay, 2018, 2019a, 2019b). In a previous study (Chapter 2), I established that yellow mongooses in an urban location could solve a novel task of increasing complexity. Since mongooses are able to learn to solve a novel problem in a rapidly changing urban environment, I expected that they would have some level of cognitive flexibility, allowing them to alter their behaviour based on changes in their environment.

I assessed whether yellow mongooses in my study area exhibited cognitive flexibility through two experimental designs: (1) reversal learning experiments and (2) attention task experiments, both of which had not previously been tested in yellow mongooses (and little is known about their cognitive abilities in general). I hypothesised that the urban yellow mongooses would exhibit evidence of cognitive flexibility by learning to inhibit a previously learned response (reversal learning), as well as solving a problem in the presence of distraction (attention task). I assessed whether yellow mongooses were capable of associative learning by assessing changes in their latency to consume the preferred food and success rates over trials, and predicted a decrease in the latency to consume a preferred food item and an increase in success rate over successive trials as mongooses would successfully learn which box contained the preferred food item. I also assessed whether mongooses were capable of reversal learning by assessing changes in their latency to consume the preferred food and success rates over trials, and predicted an increase in the latency to consume the preferred food item directly following the reversal (since at least one error is expected directly following a reversal; Mackintosh et al., 1968) with a decrease over the successive trials. Similarly, I expected a decrease in the success rate directly following the reversal with an increase over the successive trials as mongooses would at first behave according to the initial association but successfully relearn which box contained the preferred food item. In addition,

I established whether yellow mongooses could divide their attention between two tasks (problem-solving and vigilance) by successfully solving a problem in the face of distraction. I predicted that mongooses would successfully divide their attention by solving the puzzle box problem while remaining vigilant at every level of distraction. I assessed whether the level of human contact was associated with the mongooses' cognitive flexibility. I predicted that their reversal learning ability and attention would not differ between two locations with different levels of human presence or with the proximity to human residents since I previously showed that problem-solving abilities did not differ between the two study locations (Meyersdal estates; Chapter 2).

MATERIALS AND METHODS

Study area

This study took place at two locations in the urbanised Meyersdal area south of Johannesburg. The Meyersdal Nature Estate (26°18'08.2 "S 28°04'55.9 "E; 300 ha) consisted of a residential area and a separate, fenced-off nature area where the yellow mongoose colonies were located, whereas the Meyersdal Eco Estate (26°17'03.6"S 28°04'50.8"E; 480 ha) had no fenced-off nature area, and instead, the mongoose colonies were dispersed throughout the residential area. The two locations were separated by a double-laned tar road that the yellow mongooses rarely crossed (Cronk and Pillay, 2021). A total of ten sites were selected for this study, five in the Nature Estate and five in the Eco Estate. The sites were selected based on the regular occurrence of yellow mongooses and a distance of at least 200 m from any other site to ensure independent colonies since urban yellow mongooses' home ranges are approximately 0.13 km^2 on average (Cronk and Pillay, 2019a, 2021).

Experimental design and protocol

Clear Perspex puzzle boxes were used for both experiments in this study. The puzzle boxes consisted of a lid that could be opened and closed via hinges. Meat offcuts (1 teaspoon) were placed inside the box as an incentive to solve the problem. The boxes also had small holes along the sides and top to allow mongooses to detect the food incentives inside the box via olfactory cues (in addition to the visual cues through the clear box). This study took place between April and December 2020. As a result of the time elapsed since mongooses first solved the puzzle box problem, as well as two new sites that were not used previously

(Chapter 2), the mongooses were trained to open the puzzle boxes at all sites. This included two stages: stage 1, where the mongooses were exposed to a puzzle box with an open lid allowing for habituation, and stage 2, where mongooses were exposed to a puzzle box with a mostly closed lid propped up with a stick, leaving a 1 cm opening. The mongooses had to obtain the food incentive from the puzzle box successfully for a total of five trials at stage 1 before proceeding to stage 2. After the mongooses successfully obtained the food incentive from the puzzle box at stage 2 for a total of five trials, the lids of the puzzle boxes were closed entirely, and the experiments commenced.

Reversal learning

For the reversal learning experiment, mongooses underwent two learning phases: an associative learning phase and a reversal learning phase. During the associative learning phase, mongooses were trained to associate a specific puzzle box with either a preferred or non-preferred food incentive. Two puzzle boxes with closed lids were placed next to each other (the width of one puzzle box apart). The puzzle boxes were distinguishable based on two factors: 1) a visual cue; and 2) location. For the visual cue, two differently shaped objects (a small plastic animal figurine and a pebble of a similar size obtained from the immediate environment) were attached to the lid of each box, respectively, providing the mongooses with a distinct visual difference between the two boxes. A second cue, spatial discrimination, was used due to uncertainty regarding the visual perception of yellow mongooses. For the spatial cue, the boxes remained in the same position throughout this study, allowing mongooses to use their position in the environment as an additional cue to tell the boxes apart (Figure 1a). Two separate food incentives were used: a preferred food item and a non-preferred food item. Consistent with Cronk and Pillay (2018), a pilot study conducted prior to this experiment revealed that urban yellow mongooses preferred meat which was selected as the preferred food item. However, in contrast to Cronk and Pillay (2018) who found that bread was the second-most preferred food item in urban yellow mongooses, the pilot study revealed that mongooses rarely consumed bread. Thus it was selected as the appropriate non-preferred food item, especially since there are records of mongooses consuming this food type. The preferred food item was placed in the first box, and the non-preferred food item in the second box. This was kept consistent for the duration of this associative learning phase. To ensure that the mongooses did not choose the puzzle box based on olfactory cues, the holes in the puzzle boxes were covered for the duration of this experiment, and both boxes

were exposed to the scent of both food items before each trial. Since the puzzle boxes were transparent, the food types were visible. However, every care was taken to ensure that the food types appeared similar, by using thin slices of a light-coloured deli meat and bread pieces of a similar thickness. Additionally, both food items were presented in the same manner by dividing the food into similarly sized pieces and spreading it out across the bottom of the puzzle box (which was mostly obscured by surrounding vegetation).

The experimental set-up occurred between 06h00 and 12h00 daily when yellow mongooses were the most active (Cronk and Pillay, 2019a, 2020). After the initial set-up at one site was completed, the same experiment was set up at the other sites (i.e. the experiment was conducted at all sites simultaneously). The experiment was reset daily at all sites minimising the time between trials. Each site was visited twice per day (between 06h00 and 12h00) and reset if the mongooses had consumed the food during the previous trial. This allowed for a maximum of two trials per site per day. Resetting the experiment involved clearing out any leftover food from the puzzle boxes and replenishing the same boxes with fresh food incentives. The same puzzle boxes were used for the duration of the experiment at each site (unless the puzzle box was destroyed by large herbivores or removed by human residents, in which case it was replaced by a new puzzle box).

The mongooses were exposed to both boxes simultaneously. However, the first box contacted by a mongoose was considered the box chosen by the mongoose during the particular trial. Browning® Trail Cameras (Model BTC-8A; 55° field of view; Browning, 2019) triggered with a motion sensor were set up between 1 and 2 m away from the experiment with an unobstructed view of the puzzle boxes. Each trial started as soon as a mongoose entered the camera's field of view (1 – 2 m across) and ended as soon as the mongoose consumed the preferred food item. From the video footage, the box contacted, opened, and the food consumed first was recorded. Individual trials were recorded as successful (box containing preferred food item was contacted first, opened first, and food consumed first), successful with error (box containing non-preferred food item contacted first, whereafter the mongoose opened the box containing preferred food item and consumed the preferred food item), or unsuccessful (box containing non-preferred food item opened before box containing preferred food item). From the camera trap footage, the number of successful, successful with error, and unsuccessful trials were recorded. The latency to consume the preferred food reward was recorded for each trial as the number of seconds elapsed from the moment the mongoose entered the camera's view until it consumed the preferred food item. The box contacted and opened first, and the food item consumed was

recorded. Mongooses had the opportunity to visit both boxes during every trial, even if they selected the box with the non-preferred food item first. Trials that were successful with error were considered successful as mongooses were able to correct their behaviour after contacting the incorrect box initially. The learning criterion consisted of 7 correct choices out of 10 consecutive trials by an individual mongoose. Once this criterion was reached, the associative learning phase was terminated, and the reversal learning phase commenced.

During the reversal learning phase, the food items in the boxes were reversed. In other words, the box previously containing the preferred food now contained the non-preferred food, and vice versa (Figure 1b). The same criterion as the previous phase was used (7 correct selections out of 10 consecutive trials). Once again, the number of successful, successful with error, and unsuccessful trials, the latency to consume the preferred food, the box visited first, and the food item consumed first was recorded. This allowed me to assess whether mongooses were capable of reversal learning. The straight-line distance between each site and the nearest human residence was measured using Google Earth™ and used as a measure of the effect of human resident proximity on the reversal learning abilities of yellow mongooses.

A control test, similar to the one by Lucon-Xiccato and Bisazza (2014), was performed before the experiments were concluded at eight of the ten sites to validate the experimental design that mongooses were using the visual cues provided to select a puzzle box rather than olfactory cues to determine which box contained the preferred food item. In this control test, the same experiment was done (with one box containing the preferred and the other a non-preferred food type), but the puzzle boxes both had no object, and their position/orientation was randomly set (Figure 1c). Therefore, the visual and spatial cues of the boxes were not obvious. From this test, I ascertained whether the mongooses selected the box containing the preferred food incentive more often than predicted by chance indicating the use of an olfactory cue for decision-making.

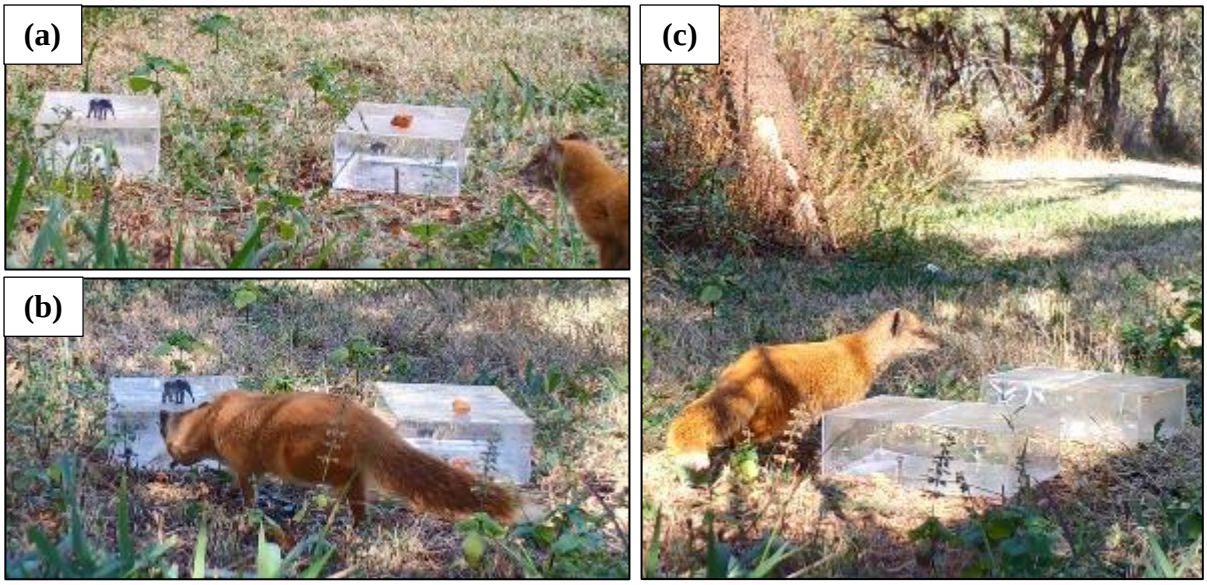


Figure 1. The experimental set-up of a reversal learning experiment conducted on yellow mongooses. **(a)** An associative learning phase where the left-most box contained the preferred food type (meat) with a small animal figurine on the lid of the box providing a visual cue, and the right-most box contained the non-preferred food type (bread) with a small pebble on the lid of the box providing a visual cue. **(b)** Reversal learning phase where the preferred and non-preferred food items were reversed so that each box contained the opposite food item (bread left and meat right), and **(c)** a control where the orientation of the boxes is changed, the objects removed from the lids, and the placement of the two food items randomised.

Attention task

The attention task experiments were conducted directly following the reversal learning experiments at the same sites (the same focal individuals participated in both experiments as confirmed using facial recognition technology; School of Computational and Applied Mathematics, University of the Witwatersrand). For the attention task experiment, mongooses were again provided with a single puzzle box with the lid closed containing only one food incentive (meat). Zero, one, two, or three distraction objects were placed around the box, providing the mongooses with varying levels of distraction. The distraction objects consisted of a stick nailed to the ground, with shiny silver strips of plastic attached to the stick. The silver strips moved with the wind, providing the mongooses with unpredictable distractions while engaged with the puzzle box (Figure 2). The position in which the distraction objects were placed around the box, as well as the number of objects, was changed randomly for each trial to avoid the mongooses habituating to the objects. Each level of distraction was repeated for a total of three trials per distraction level at each site (i.e. a total of 12 trials per site). This experiment was set up at all sites daily and revisited once per day to replenish the food incentive (this allowed for a maximum of two trials per site per day).

From camera trap footage, the latency to consume the food incentive was recorded for every trial to ascertain whether mongooses were able to efficiently solve the puzzle box task while experiencing distractions. Additionally, I recorded the frequency of vigilance behaviour (defined as the ceasing of all activity; alert; listening and staring in a particular direction; scanning the environment; and standing upright on hind legs). Finally, I used the straight-line distance between each site and the nearest human residence (measured using Google Earth™) to assess whether the proximity of human residents was associated with the problem-solving abilities of yellow mongooses during distraction.

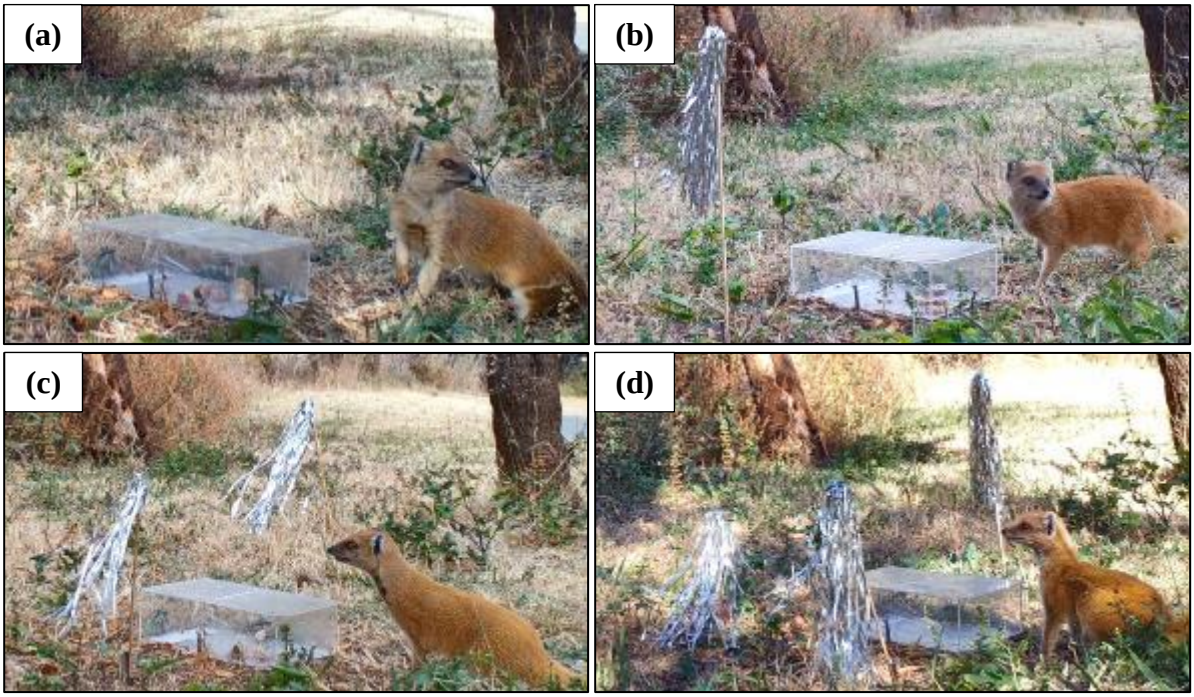


Figure 2. The experimental set-up of an attention task experiment conducted on yellow mongooses with **(a)** zero, **(b)** one, **(c)** two, and **(d)** three distractions surrounding the puzzle box. The number of distractions surrounding the puzzle box and the position of each distraction were randomised with each trial.

Yellow mongooses are predominantly solitary foragers (le Roux et al., 2008; Manser et al., 2014), and as a result, the same focal individual consistently visited the experiments (confirmed using facial recognition software; School of Computational and Applied Mathematics, University of the Witwatersrand). Only adult mongooses participated in this study, and juveniles never attempted to solve the puzzle box problem. Males and females could not be distinguished due to yellow mongooses' lack of sexual dimorphism, and therefore sex was not considered in this study. Furthermore, the Meyersdal management did not approve the collaring or marking of individuals in this study.

Data analyses

All statistical analyses were conducted using R Statistical Software (R version 3.4.3; R Core Team, 2013). Shapiro-Wilk tests were used to test for normality. Non-normal variables were transformed using a Box-Cox transformation (R package: MASS), and if variables did not normalise after transformation, non-parametric tests were used. For the reversal learning experiment, a linear mixed effect model (LMER; R packages: lme4, lmerTest) was used to analyse differences in the latency to consume the preferred food item with location and treatment (learning phase). The two treatments were a repeated measures design, with location and treatment as fixed effects, trial and site as random factors, and the proximity to human residents as a covariate. A binomial regression (GLM; family = Binomial, link = logit) was used to determine what factors (location, learning phase, latency to contact the correct box, latency to open the correct box, latency to consume the preferred food, proximity to nearest human residents) were associated with success versus error. A Tukey post hoc test was used to determine pairwise differences for significant fixed factors (general linear hypothesis; R package: multcomp). The success rate was calculated as a percentage of the number of sites with a successful trial out of the number of sites per trial.

For the attention task experiment, a generalised linear mixed effects model (GLMM) was used to analyse differences in the (i) latency to investigate the puzzle box (family = Gaussian; link = log) and (ii) vigilance frequency (family = Poisson; link = log), and a linear mixed effect model (LMER) to analyse the difference in (iii) latency to consume the food incentive with the different levels of distraction at the two locations. The various treatments (number of distraction objects) were a repeated measures design, with location and treatment as fixed effects, trial and site as random factors, and the proximity to human residents as a covariate. A Tukey post hoc test was used to determine pairwise differences for significant fixed factors (general linear hypothesis; R package: multcomp). A Spearman's rank correlation was used to analyse whether the latency to consume the food incentive was significantly correlated with the vigilance frequency.

Ethical approval

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2020/09/05/A).

RESULTS

Cognitive flexibility was assessed in an urban population of yellow mongooses (n = 10) by providing them with reversal learning and attention task experiments.

Reversal learning experiment

Latency to consume

The latency to consume the preferred food type was defined as the number of seconds that elapsed from the moment the mongoose entered the camera's view until it consumed the preferred food item. This was considered an indication of the mongooses' learning ability. Location ($\chi^2 = 2.27$, df = 1, p = 0.132; LMER), learning phase (associative versus reversal; $\chi^2 = 1.65$, df = 1, p = 0.199), and the interaction between location and the learning phase ($\chi^2 = 0.91$, df = 1, p = 0.341) were not significant predictors of the latency to consume. I predicted that the latency to consume the preferred food type would be longer during the first trial of each phase and decrease during subsequent trials as the mongooses learned which box contained the preferred food type. In each location, the mean latency to consume (s) the food for all sites generally decreased over the trials and during each treatment (Figure 3). During the associative learning phase, the latency to consume the food was the highest in the Eco Estate compared with the Nature Estate during the first and last trials, but the latency decreased to below the initial latency for the final trial in each location. During the reversal learning phase, the latency to consume the food was initially similar to the first trial of the associative learning phase, but longer than the final trial of the associative learning phase. The latency to consume further decreased more rapidly in the Eco Estate than the Nature Estate and was lower during the final trial in the Eco Estate than in the Nature Estate. The latency to consume the food during the final trial of the reversal learning stage in the Nature Estate was lower than it was during the initial trial in the same location. However, it should be noted that from trial 13 onwards, the latency to consume in this location was affected by one site only where the success criterion had not yet been reached.

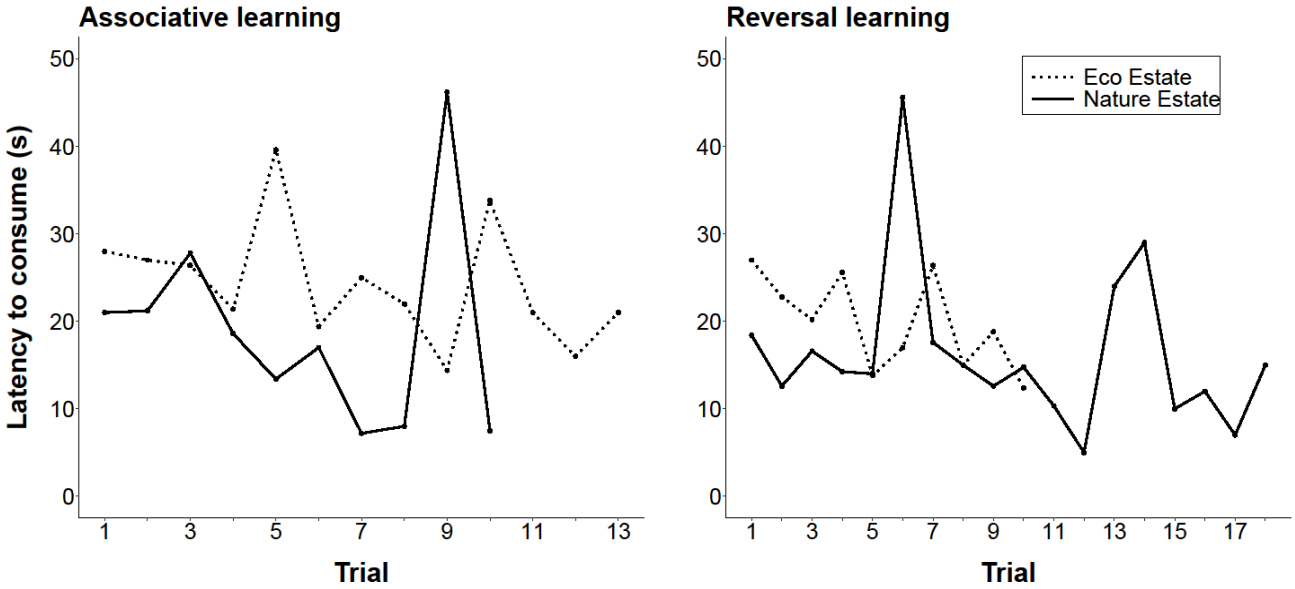


Figure 3. The mean latency to consume (s) the preferred food item by yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate during the associative and reversal learning phases of a reversal learning experiment.

Success counts and success rates

A binomial regression revealed that the latency to contact the box containing the preferred food item ($\chi^2 = 6.42$, df = 1, p = 0.011) and the latency to open the box containing the preferred food item ($\chi^2 = 6.04$, df = 1, p = 0.014) were significant predictors of success. In addition, the latency to contact the box containing the preferred food item was shorter during successful trials in both the associative and reversal learning phases (Figure 4).

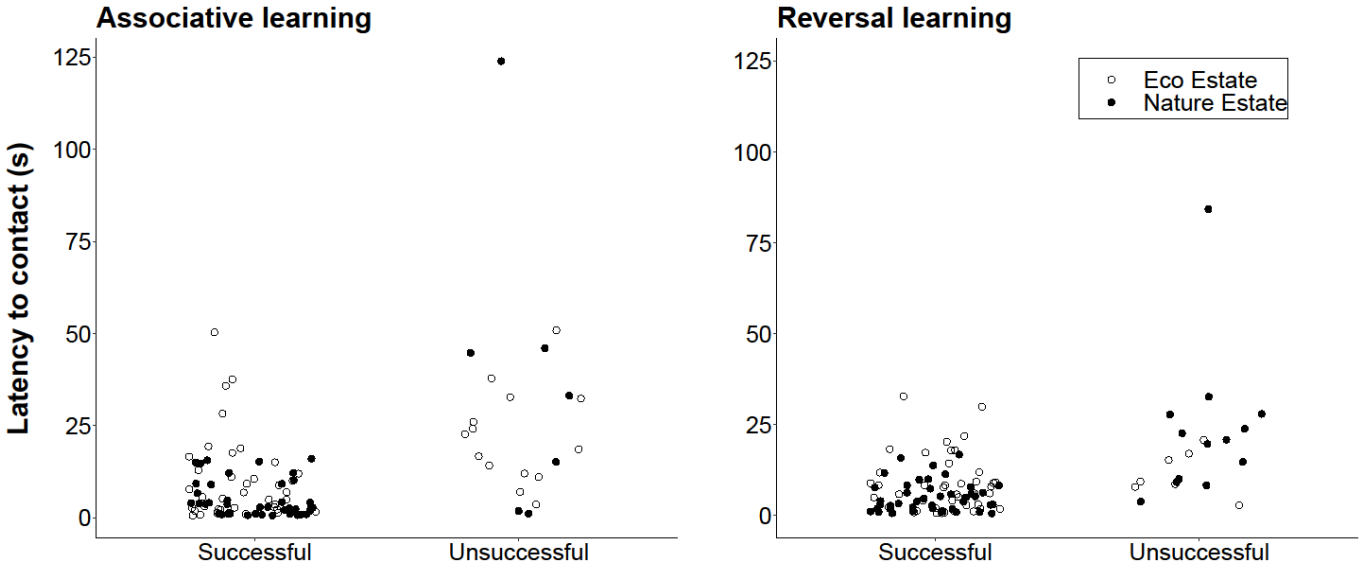


Figure 4. The latency (s) of yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate to contact the puzzle box containing the preferred food item during successful and unsuccessful trials at the associative learning and reversal learning phases of a reversal learning experiment.

The latency to open the box containing the preferred food item was similarly shorter during successful trials during both the associative and reversal learning phases (Figure 5). Thus, when mongooses made a quicker decision between the two boxes, they were more likely to make the correct choice.

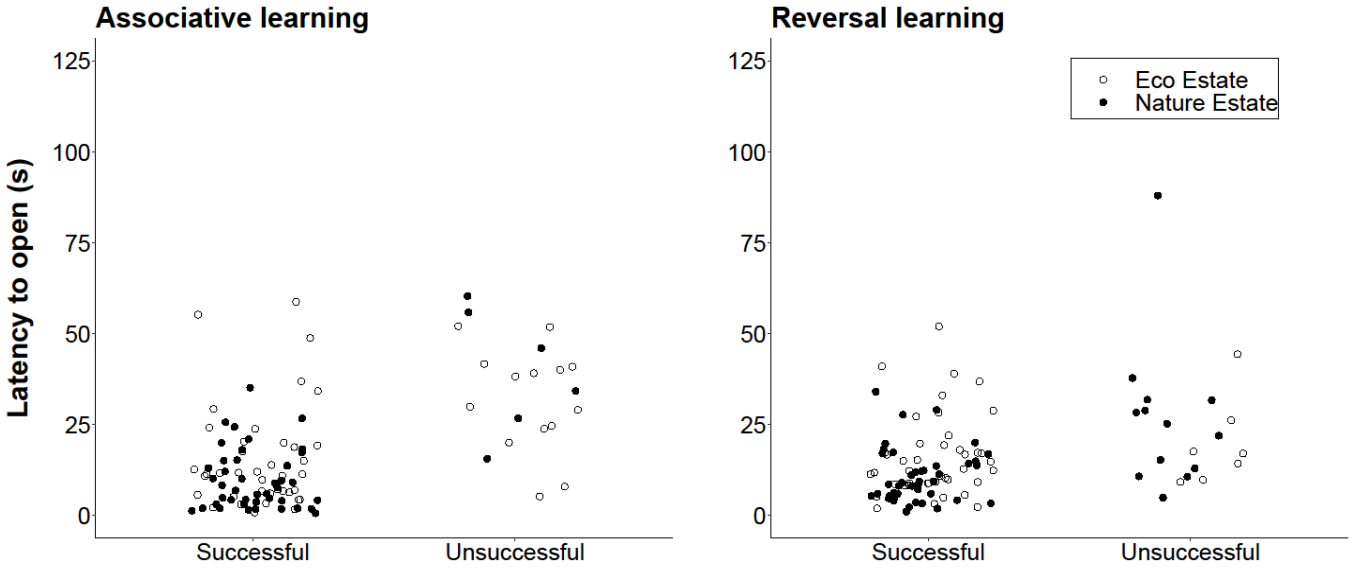


Figure 5. The latency (s) of yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate to open the puzzle box containing the preferred food item during successful and unsuccessful trials at the associative learning and reversal learning phases of a reversal learning experiment.

In order to investigate the patterns of success over the various trials, I calculated the success rate as a percentage using the proportion of successful trials at each location (Figure 6). The success rate differed between the two locations and over the various trials. During the associative learning phase, mongooses reached the 70% success rate criterion at ten trials in the Nature Estate and 13 trials in the Eco Estate. Mongooses in the Nature Estate had a 100% success rate at all sites during the first trial, which dropped to 60% during trials 2 and 3, and fluctuated between 60% and 100% for the remainder of the trials. In the Eco Estate, mongooses initially had an 80% success rate which decreased to 40% over the first five trials. After that, their success rate increased until they reached 100% success at trial 11 and maintained this success rate for the remainder of the trials. During the reversal learning phase, mongooses reached the 70% success rate criterion at 18 trials in the Nature Estate and ten trials in the Eco Estate. In the Nature Estate, the mongooses' success rate dropped from 80% during the last trial of the associative learning phase to 40% during the first trial of the reversal learning phase. Thereafter the success rate fluctuated between 40% and 100% until they reached 100% at all sites during consecutive trials at trials 11 – 12 and again at trials 15 – 18. In the Eco Estate, mongooses maintained their 100% success rate from the last trial of the associative learning phase during the first trial of the reversal learning phase. During trial 2, the success rate dropped to 40%, whereafter it fluctuated between 80% and 100% for the remainder of the trials.

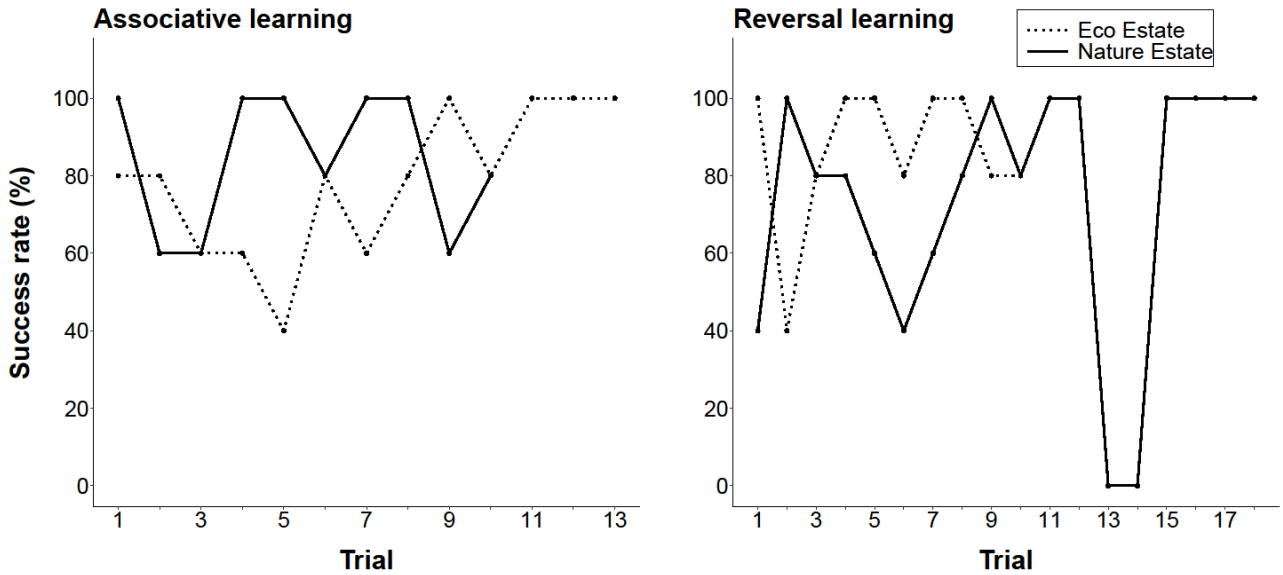


Figure 6. The percentage success by yellow mongooses in the Meyersdal Eco Estate and Meyersdal Nature Estate for each trial during the associative learning and reversal learning phases during a reversal learning experiment.

Attention task experiment

Latency to investigate

Location ($\chi^2 = 0.01$, df = 1, p = 0.905; GLMM), the number of distractions ($\chi^2 = 7.60$, df = 3, p = 0.055), and the interaction between the location and the number of distractions ($\chi^2 = 1.40$, df = 3, p = 0.7045) were not significant predictors of the latency to investigate the puzzle box. This indicated that mongooses were not fearful of approaching the puzzle boxes even when distractions were present.

Latency to consume

The number of distractions present at the puzzle box was the only significant predictor of the latency to consume the food ($\chi^2 = 10.92$, df = 3, p = 0.012; LMER; Figure 7). Location ($\chi^2 = 1.20$, df = 1, p = 0.273), proximity to human residents ($\chi^2 = 0.24$, df = 1, p = 0.626), and the interaction between the location and number of distractions ($\chi^2 = 6.32$, df = 3, p = 0.097) were not significant predictors of the latency to consume the food. The latency to consume the food incentive was significantly longer when two (z = 2.59, p = 0.047) and three (z = 3.08, p = 0.011) distractions were present compared with when zero distractions were present (Figure 7).

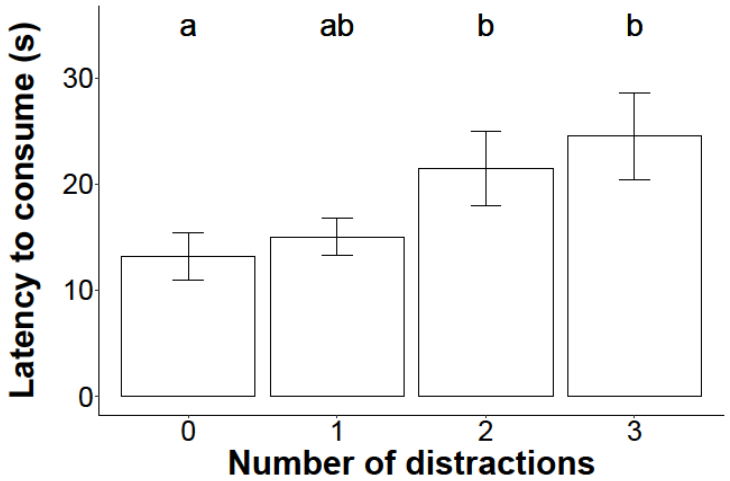


Figure 7. The latency to consume (s) a food incentive by yellow mongooses during puzzle box experiments with 0, 1, 2, and 3 distractions present. Error bars indicate standard error. The same alphabet letters indicate no significant difference in the number of distractions.

Vigilance

The frequency at which mongooses were vigilant differed significantly with the number of distractions (χ^2 = 23.59, df = 3, p < 0.001; GLMM; Figure 8) but not with location (χ^2 = 2.25, df = 1, p = 0.134) or the interaction between the number of distractions and location (χ^2 = 6.49, df = 3, p = 0.090). Mongooses were significantly more vigilant when three distractions were present compared with zero distractions (z = 2.77, p = 0.028; Figure 8).

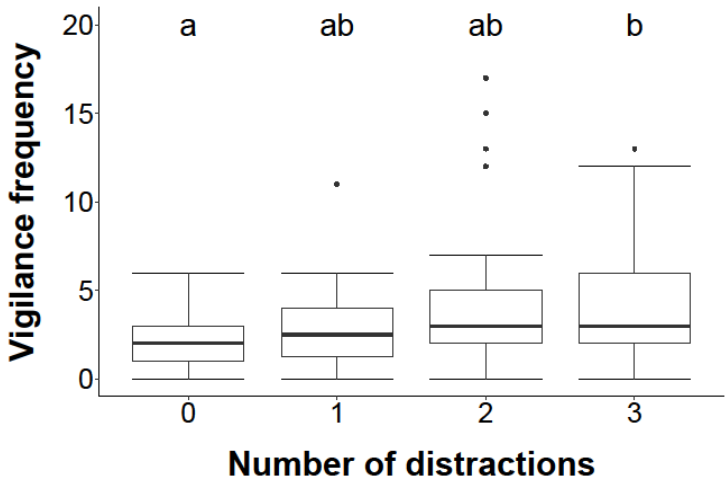


Figure 8. The frequency of vigilance behaviour displayed by yellow mongooses at four levels of distraction during an attention task experiment. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference in the number of distractions.

There was a significant, strong positive correlation between the latency to consume (s) and the frequency at which mongooses displayed vigilance behaviour (r_s = 0.63, p < 0.001; Figure 9). As the vigilance frequency increased, so did the latency to consume.

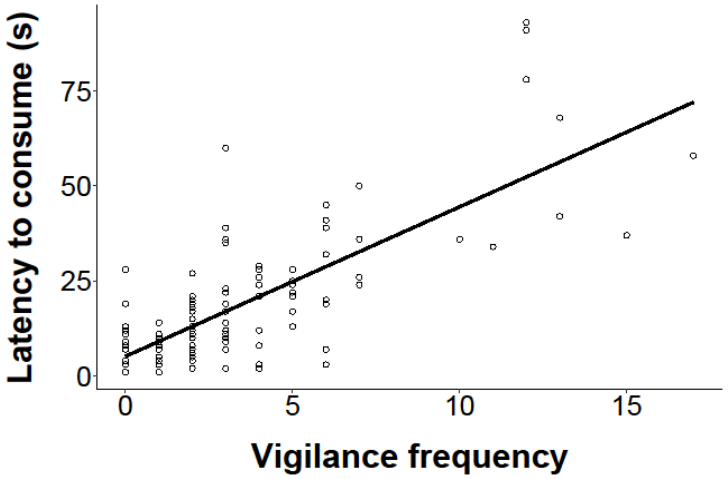


Figure 9. The relationship between the latency to consume the food incentive and the frequency of being vigilant by yellow mongooses during an attention task experiment. The trendline is significant ($p < 0.001$; Spearman rank test).

Control test

A control test was conducted to ensure that mongooses used visual and spatial cues to select the appropriate puzzle box and not olfactory cues to locate the preferred food item. When all visual cues were removed from the boxes, and the boxes' orientation changed, mongooses only had two out of eight successful trials (25%; Table 1) to obtain the food incentive. One trial was unsuccessful (12.5%), and most trials were successful with an error (i.e. mongooses contacted the incorrect box first, after which they corrected to opening the correct box; five trials; 62.5%). This indicated that mongooses used visual cues mainly, and possibly not olfactory cues, to locate boxes in the reversal learning experiment. Only after contacting the box containing the non-preferred food item did mongooses shift to the box containing the preferred food item. Thus, the initial decision between the two boxes was made before the mongooses contacted the box, indicating a lack in the use of olfactory cues for decision-making.

Table 1. The percentage trials (number of trials/total trials) that were successful, successful with error, and unsuccessful during a control and testing phase of a reversal learning experiment.

Treatment	Control	Test	
		Associative learning	Reversal learning
Successful	25.0 (2/8)	59.2 (60/103)	54.5 (60/110)
Successful with error	62.5 (5/8)	19.4 (20/103)	26.4 (29/110)
Unsuccessful	12.5 (1/8)	21.4 (22/103)	19.1 (21/110)

DISCUSSION

Reversal learning and attention task experiments were conducted to assess whether a population of urban-dwelling yellow mongooses are cognitively flexible. During reversal learning experiments, mongooses were capable of learning an association between a cue (visual and spatial) and a preferred food incentive. They were further capable of reversal learning, where they unlearned a previous association and, in its place, learned a new association to continually obtain the preferred food incentive. Mongooses' learning during the two learning phases was exhibited by a general decrease in the latency to consume the preferred food and a general increase in the success rate over successive trials. Mongooses were quicker at contacting and opening the puzzle box, but no quicker at consuming the preferred food during successful trials than unsuccessful ones. During the attention task experiments, mongooses were able to solve the puzzle box problem at every level of distraction, but took longer to solve the puzzle box problem, and were vigilant more frequently, when there were two or three distractions compared with no distractions. In addition, the duration of solving the problem was correlated with the vigilance frequency so that when mongooses were vigilant more frequently, they performed worse at the puzzle box task.

Animals may make use of various rule-based strategies when solving a reversal learning task: (1) make the correct choice and then continue to make the same correct choice in the subsequent trial (win-stay strategy), (2) make the correct choice and then change to the incorrect choice in the subsequent trial (win-shift strategy), (3) make the incorrect choice and then change to the correct choice in the subsequent trial (lose-shift strategy), and (4) make the incorrect choice and then continue to make the same incorrect choice in the subsequent trial (lose-stay strategy). Reversal learning requires a win-stay, lose-shift strategy (Nowak and Sigmund, 1993; Buechel et al., 2017). In other words, if the outcome of any given stimulus is

a reward, an individual should stay and interact with the stimulus to be rewarded consistently. If, however, the outcome is no longer rewarded, the individual should move to the alternative to increase its chances of being rewarded. However, even in the most successful case, this strategy would require an animal to make at least one error immediately following the reversal (Nowak and Sigmund, 1993; Buechel et al., 2017).

During reversal learning experiments, mongooses had the opportunity to use visual and spatial cues to select a puzzle box containing either a preferred or non-preferred food type. A successful trial was any trial during which the mongoose opened the puzzle box containing the preferred food type before the one containing the non-preferred food type. The latency to consume the food was a measure of the duration of completing the task, in other words, the time taken to consume the preferred food type. As predicted, the mongooses generally had longer latencies during the first trial of each learning phase compared with the final trial of each phase, indicating that they were able to solve the problem faster over successive trials. The longer latencies initially were expected since the mongooses were more likely to make mistakes during the first few trials, spending time investigating each box or making incorrect choices, thus increasing the latency to consume the preferred food after correcting their response. This improvement in problem-solving speed possibly indicates learning in which the mongooses were able to select the correct box quicker by using the visual and spatial cues as associations. The increase in the latency to consume the food during the first trial of the reversal learning phase (compared with the final trial of the associative learning phase) indicated that mongooses likely spent more time locating the correct box due to visiting the previously rewarded box initially. However, after mongooses learned that the alternative box contained the preferred food item, the latency decreased again over the successive trials.

Assessing successful versus unsuccessful trials allowed me to establish what factors influenced success during individual trials. The latency to contact and open the correct box was shorter during successful trials than during unsuccessful trials. Thus, when mongooses chose between the boxes quicker, they were more likely to select the correct box. This may indicate that the mongooses learned to use the visual (objects) and spatial (orientation) cues to select the correct box even before approaching the boxes. However, the latency to consume the food reward was not associated with the trial's success. This suggests that mongooses were no quicker to consume the preferred food item during successful trials than during unsuccessful ones. Therefore, it is possible that mongooses quickly corrected their choice after opening the incorrect box and shifted to the correct box.

In the associative learning phase, I expected that the mongooses' success rate would initially be low and increase over time as mongooses learned which box contained the preferred food item. I also expected a lower success rate directly following the reversal, since animals are likely to make at least one mistake directly following a reversal when using rule-based strategies, after which this probability will decrease (Mackintosh et al., 1968). The mongooses' success rate was generally the lowest between the first two trials of each learning phase, and then it largely increased or fluctuated between 80% and 100%. In some cases, there was a significant drop in success rate for a single trial, but the success rates were never below 40% (it should be noted that the significant drop in success rate during the reversal learning phase in the Nature Estate was attributed to the fact that a mongoose at only one site required more than 13 trials to reach the success criterion, resulting in a 0% success rate overall when the individual trial at this particular site was unsuccessful). The mongooses thus had a high success rate overall and appeared to learn the rule of the task within the first few trials.

Cognitive style, the manner in which an individual approaches a specific problem (which differs from general cognitive ability that can be identical in individuals with different cognitive styles), often involves trade-offs (Bebus et al., 2016; Mazza et al., 2018). For example, some individuals may be better at learning initial associations, whereas those who take longer to learn an initial association may be more flexible and perform better at a reversal learning task (e.g. Mazza et al., 2018). Similarly, animals may show a speed-vs-accuracy trade-off, where successfully solving a problem requires more time, and solving a problem quicker can lead to more errors (e.g. Mazza et al., 2018). The mongooses in my study did not show any such trade-offs. The overall performance during associative learning and reversal learning was comparable, suggesting that mongooses did not experience proactive interference and instead used rule-based strategies for reversal learning success. Furthermore, the mongooses did not exhibit a speed-vs-accuracy trade-off and instead were more likely to approach the correct puzzle box quicker when using visual and spatial discriminations. The duration of completing the puzzle box task was similar between successful and unsuccessful trials, likely because mongooses were quick to correct incorrect choices during unsuccessful trials.

Attention task experiments were conducted to assess whether mongooses were capable of dividing their attention between two tasks – solving a puzzle box problem and remaining vigilant in the face of distraction. The mongooses solved the puzzle box problem at all levels of distraction, indicating that they could engage in cognitively demanding

activities despite being surrounded by distractions. However, mongooses were only distracted by the artificial distractions surrounding the puzzle box when the level of distraction was high. The mongooses took the longest to solve the puzzle box problem when there were two or three distractions surrounding the box, and they were the quickest when there were no distractions. It appears that mongooses did not utilise selective attention since the distraction level did influence their problem-solving speed, suggesting an inability to filter out the distraction (Zentall, 2005; Carlson et al., 2018). Instead, mongooses more likely divided their attention between the two tasks (problem-solving and vigilance), or they were alternating their attention by rapidly shifting their attention between the two tasks. To understand their processing of the stimuli, it is necessary to investigate their performance at both tasks.

The frequency of performing vigilance behaviour was the highest with the most distraction and the lowest with no distraction. When there were two distractions, mongooses were no more vigilant than when there were zero distractions, yet they took significantly longer to solve the problem with two distractions than at zero distractions. However, with three distractions, mongooses both performed worse at problem-solving and were vigilant more frequently. This raises the question: were mongooses experiencing cognitive deficits when solving the problem whilst being distracted because they were dividing their attention between the two tasks, or did they simply take longer to solve the problem because they were spending more time being vigilant? To answer this question, I correlated the duration of completing the task and the frequency of vigilance. When mongooses were more vigilant, they also took significantly longer to solve the puzzle box problem. If mongooses used divided attention at high levels of distraction, I would have expected worse performance at the puzzle box task, but no change in vigilance frequency (similar to the results observed at two distractions), with more distractions, and no correlation between the latency to consume and vigilance frequency. This is because divided attention involves the simultaneous processing of both stimuli, which would have resulted in considerably lower vigilance scores since vigilance involves the termination of all other activities. Instead, the correlation between the vigilance and latency to consume concurs with the description of alternating attention, where an individual terminates focus on one task in favour of another and rapidly shifts their attention back and forth between the two tasks (Commodari, 2017). In doing so, the time spent on one task would influence the time spent on the other, since the focus is only on one task at a time. Similarly, an increase in the distractions was expected to increase vigilance frequency, which, in turn, would increase the latency to solve the puzzle box problem since mongooses shifted their attention towards and away from the puzzle box

problem, as observed with three distractions. A definite conclusion regarding the attentional mechanism utilised by mongooses in this study (divided versus alternating attention) would be implausible without speculation, although mongooses were evidently capable of focusing their attention on two tasks (solving the puzzle box task and remaining vigilant) successfully. This ability to prioritise the processing of stimuli as it becomes relevant in the environment, by focusing on, and switching between tasks, suggests cognitive flexibility (Diamond, 2013).

Cognitive flexibility is closely linked with two aspects of memory: short-term memory and working memory. The use of rule-based strategies to solve reversal learning tasks (i.e. win-stay, lose-shift) requires adequate short-term memory as the individual has to remember which stimulus was previously rewarded (Buechel et al., 2018), and the success of each trial will depend on the animal's memory of the previous trial (Gonzalez et al., 1967; Kamil, 1985. In litt: Buechel et al., 2017). For example, when corvids and monkeys were presented with a reversal learning task, they were less successful at solving the task with increased time between successive trials (Kamil, 1985. In litt: Buechel et al., 2017). Thus, cognitive flexibility may not exclusively depend on the ability to learn, but may be coupled with the ability to retain newly acquired information (Gonzalez et al., 1967; Croston et al., 2016). Working memory has a limited capacity and may further be important in reducing proactive interference (Diamond, 2013). Due to this limited capacity, limitations in working memory may result in processing deficits and reduced performance during divided attention, or inhibit divided attention altogether. As a result, the ability to divide attention increases with reduced task similarity (McLeod, 1977), more practice (Spelke et al., 1976), and reduced task difficulty (Sullivan, 1976). It is possible that the mongooses I studied may have used selective attention and divided (or alternating) attention in different circumstances, especially since these two types of attention do not use different brain processes, at least in humans (Hahn et al., 2008). For example, mongooses may have used divided attention when the level of distraction was intermediate (two distractions) but switched to alternating attention as the distractions increased (three distractions), or they may have used divided/alternating attention initially but switched to selective attention as it becomes more apparent over time that the distractions pose no threat. In this way, switching between the mechanisms of attention may further indicate cognitive flexibility in urban yellow mongooses, although this was not tested in the present study.

Cognitive flexibility is the ability to switch between task rules or shift attention between tasks, adjusting one's behaviour accordingly (Scott, 1962; Diamond, 2013). Overall, the mongooses in my study showed evidence of cognitive flexibility by means of two

common experimental indicators: the ability to learn, and switch between, task rules during reversal learning experiments, and the ability to shift attention to relevant environmental cues as their priorities change during attention task experiments. Not only were they capable of simple associative learning, but they could further learn to solve a reversal learning task. Furthermore, these mongooses were capable of solving a puzzle box problem in the face of many distractions, likely through splitting their attention between the tasks, but their task performance declined with sufficient distraction. The results from these two experiments did not differ between the two locations, indicating that the level of human disturbance had no effect on their cognitive flexibility. Being cognitively flexible allows mongooses to adapt their learned responses to environmental changes and focus their attention on various relevant environmental stimuli simultaneously, which may contribute to their success in urban habitats.

REFERENCES

Bebus, S. E., Small, T. W., Jones, B. C., Elderbrock, E. K., & Schoech, S. J. (2016). Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Animal Behaviour*, *111*, 251–260. doi: 10.1016/j.anbehav.2015.10.027

Bennett, M. S. (2021). What behavioral abilities emerged at key milestones in human brain evolution? 13 hypotheses on the 600-million-year phylogenetic history of human intelligence. *Frontiers in Psychology*, *12*, 685853. doi: 10.3389/fpsyg.2021.685853

Bizani, M. (2014). *Diet of the yellow mongoose (Cynictis penicillata) in the Albany Thicket Biome of South Africa* (Master of Science). University of Fort Hare.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, *121*(4), 372–379. doi: 10.1037/0735-7036.121.4.372

Browning. (2019). *Browning Trail Cameras: Advantage SpecOps Full HD Video Model BTC-8A: Instruction Manual*. Browning. Retrieved from https://browningtrailcameras.zendesk.com/hc/en-us/article_attachments/360073084653/Spec_Ops_Advantage_BTC-8A.pdf.

Buechel, S. D., Boussard, A., Kotrschal, A., van der Bijl, W., & Kolm, N. (2017). Brain size affects performance in a reversal-learning test. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1871), 20172031. Doi: 10.1098/rspb.2017.2031

Carlson, K., Gadziola, M., Dauster, E., & Wesson, D. (2018). Selective attention controls olfactory decisions and the neural encoding of odors. *Current Biology*, *28*(14), 2195–2205. Doi: 10.1016/j.cub.2018.05.011

Commodari, E. (2017). Novice readers: The role of focused, selective, distributed and alternating attention at the first year of the academic curriculum. *I-Perception*, *8*(4), 204166951771855. Doi: 10.1177/2041669517718557

Cronk, N. E., & Pillay, N. (2018). Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethologica*, *21*(2), 127–136. doi: 10.1007/s10211-018-0291-x

Cronk, N. E., & Pillay, N. (2019a). Flexible use of urban resources by the yellow mongoose *Cynictis penicillata*. *Animals*, *9*(7), 447. doi: 10.3390/ani9070447

Cronk, N. E., & Pillay, N. (2020). Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment. *Journal of Urban Ecology*, *6*(1), 1–9. doi: 10.1093/jue/juaa013

Cronk, N. E., & Pillay, N. (2021). Home range and use of residential gardens by yellow mongoose *Cynictis penicillata* in an urban environment. *Urban Ecosystems*, *24*(1), 127–139. doi: 10.1007/s11252-020-01022-1

Cronk, N., & Pillay, N. (2019b). Dietary overlap of two sympatric African mongoose species in an urban environment. *Mammalia*, *85*(5), 428–438. doi: 10.1515/mammalia-2018-0113

Croston, R., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., Parchman, T. L., & Pravosudov, V. V. (2016). Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. *Animal Behaviour*, *123*, 139–149. doi: 10.1016/j.anbehav.2016.10.004

Diamond, A. (2013). Executive functions. *Annual Review of Psychology*, *64*(1), 135–168. doi: 10.1146/annurev-psych-113011-143750

Do Linh San, E., Cavallini, P., & Taylor, P. (2015). *The IUCN Red List of Threatened Species 2015* [Data set]. International Union for Conservation of Nature. doi: 10.2305/IUCN.UK.2015-4.RLTS.T41597A45205726.en

Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, *11*(5), 502–506. doi: 10.1093/beheco/11.5.502

Dukas, R., & Kamil, A. C. (2001). Limited attention: The constraint underlying search image. *Behavioral Ecology*, *12*(2), 192–199. doi: 10.1093/beheco/12.2.192

Federspiel, I. G., Garland, A., Guez, D., Bugnyar, T., Healy, S. D., Güntürkün, O., & Griffin, A. S. (2017). Adjusting foraging strategies: A comparison of rural and urban common mynas (*Acridotheres tristis*). *Animal Cognition*, *20*(1), 65–74. doi: 10.1007/s10071-016-1045-7

Freas, C. A., LaDage, L. D., Roth, T. C., & Pravosudov, V. V. (2012). Elevation-related differences in memory and the hippocampus in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, *84*(1), 121–127. doi: 10.1016/j.anbehav.2012.04.018

Gaalema, D. E. (2011). Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). *Journal of Comparative Psychology*, *125*(2), 246–249. doi: 10.1037/a0023148

Ginsburg, S., & Jablonka, E. (2010). The evolution of associative learning: A factor in the Cambrian explosion. *Journal of Theoretical Biology*, *266*(1), 11–20. doi: 10.1016/j.jtbi.2010.06.017

Gonzalez, R. C., Behrend, E. R., & Bitterman, M. E. (1967). Reversal learning and forgetting in bird and fish. *Science*, *158*(3800), 519–521. doi: 10.1126/science.158.3800.519

Griffiths, S. W., Brockmark, S., Höjesjö, J., & Johnsson, J. I. (2004). Coping with divided attention: The advantage of familiarity. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1540), 695–699. doi: 10.1098/rspb.2003.2648

Hahn, B., Wolkenberg, F. A., Ross, T. J., Myers, C. S., Heishman, S. J., Stein, D. J., … Stein, E. A. (2008). Divided versus selective attention: Evidence for common processing mechanisms. *Brain Research*, *1215*, 137–146. doi: 10.1016/j.brainres.2008.03.058

Hampton, R. R., Shettleworth, S. J., & westwood, R. P. (1998). Proactive interference, recency, and associative strength: Comparisons of black-capped chickadees and dark-

eyed juncos. *Animal Learning & Behavior*, *26*(4), 475–485. doi: 10.3758/BF03199241

Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H., & Holmes, A. (2017). The neural basis of reversal learning: An updated perspective. *Neuroscience*, *345*, 12–26. doi: 10.1016/j.neuroscience.2016.03.021

Kingdon, J., Happold, D., Butynski, T., Hoffman, M., Happold, M., & Kalina, J. (Eds.). (2013). *Cynictis penicillata*, Yellow Mongoose. In *Mammals of Africa. Vol. 5: Carnivores, pangolins, equids and rhinoceroses* (pp. 334–339). London: Bloomsbury.

Klanker, M., Feenstra, M., & Denys, D. (2013). Dopaminergic control of cognitive flexibility in humans and animals. *Frontiers in Neuroscience*, *7*. doi: 10.3389/fnins.2013.00201

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *308*(1135), 203–214. doi: 10.1098/rstb.1985.0020

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behaviour*, *75*(3), 943–949. doi: 10.1016/j.anbehav.2007.07.014

Leal, M., & Powell, B. J. (2012). Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters*, *8*(1), 28–30. doi: 10.1098/rsbl.2011.0480

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution*, *63*(4), 233–246. doi: 10.1159/000076784

Liu, Y., Day, L. B., Summers, K., & Burmeister, S. S. (2016). Learning to learn: Advanced behavioural flexibility in a poison frog. *Animal Behaviour*, *111*, 167–172. doi: 10.1016/j.anbehav.2015.10.018

Lucon-Xiccato, T., & Bisazza, A. (2014). Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biology Letters*, *10*(6), 20140206. doi: 10.1098/rsbl.2014.0206

Mackintosh, N. J., Mcgonigle, B., & Holgate, V. (1968). Factors underlying improvement in serial reversal learning. *Canadian Journal of Psychology / Revue Canadienne de Psychologie*, *22*(2), 85–95. doi: 10.1037/h0082753

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal Complexity in Meerkats and Other Mongoose Species. *Advances in the Study of Behavior*, *46*, 281–310. doi: 10.1016/B978-0-12-800286-5.00006-7

Mazza, V., Eccard, J. A., Zaccaroni, M., Jacob, J., & Dammhahn, M. (2018). The fast and the flexible: Cognitive style drives individual variation in cognition in a small mammal. *Animal Behaviour*, *137*, 119–132. doi: 10.1016/j.anbehav.2018.01.011

McLeod, P. (1977). A dual task response modality effect: Support for multiprocessor models of attention. *Quarterly Journal of Experimental Psychology*, *29*(4), 651–667. doi: 10.1080/14640747708400639

Mettke-Hofmann, C. (2014). Cognitive ecology: Ecological factors, life-styles, and cognition: Cognitive ecology. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(3), 345–360. doi: 10.1002/wcs.1289

Nowak, M., & Sigmund, K. (1993). A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature*, *364*(6432), 56–58. doi: 10.1038/364056a0

Papini, M. R. (2002). Pattern and process in the evolution of learning. *Psychological Review*, *109*(1), 186–201. doi: 10.1037/0033-295X.109.1.186

Parasuraman, R. (Ed.). (1998). The attentive brain: Issues and prospects. In *The Attentive Brain*. Cambridge, Mass: MIT Press.

Parker, M. O., Gaviria, J., Haigh, A., Millington, M. E., Brown, V. J., Combe, F. J., & Brennan, C. H. (2012). Discrimination reversal and attentional sets in zebrafish (*Danio rerio*). *Behavioural Brain Research*, *232*(1), 264–268. doi: 10.1016/j.bbr.2012.04.035

R Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Scott, W. A. (1962). Cognitive Complexity and Cognitive Flexibility. Sociometry, 25(4), 405. doi: 10.2307/2785779

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, *5*(1), 130–133. doi: 10.1098/rsbl.2008.0621

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Sol, D., Sayol, F., Ducatez, S., & Lefebvre, L. (2016). The life-history basis of behavioural innovations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150187. doi: 10.1098/rstb.2015.0187

Spelke, E., Hirst, W., & Neisser, U. (1976). Skills of divided attention. *Cognition*, *4*(3), 215–230. doi: 10.1016/0010-0277(76)90018-4

Stanton, L. A., Bridge, E. S., Huizinga, J., Johnson, S. R., Young, J. K., & Benson-Amram, S. (2021). Variation in reversal learning by three generalist mesocarnivores. *Animal Cognition*, *24*(3), 555–568. doi: 10.1007/s10071-020-01438-4

Sullivan, L. (1976). Selective attention and secondary message analysis: A reconsideration of Broadbent's filter model of selective attention. *Quarterly Journal of Experimental Psychology*, *28*(2), 167–178. doi: 10.1080/14640747608400549

Szabo, B., Noble, D. W. A., Byrne, R. W., Tait, D. S., & Whiting, M. J. (2018). Subproblem learning and reversal of a multidimensional visual cue in a lizard: Evidence for behavioural flexibility? *Animal Behaviour*, *144*, 17–26. doi: 10.1016/j.anbehav.2018.07.018

Tebbich, S., & Teschke, I. (2014). Coping with uncertainty: Woodpecker finches (*Cactospiza pallida*) from an unpredictable habitat are more flexible than birds from a stable habitat. *PloS ONE, 9*(3), e91718. doi: 10.1371/journal.pone.0091718

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: To be or not to be flexible, that is the question. *Animal Behaviour*, *147*, 129–136. doi: 10.1016/j.anbehav.2018.02.019

Tello-Ramos, M. C., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., & Pravosudov, V. V. (2018). Memory in wild mountain chickadees from different elevations: Comparing first-year birds with older survivors. *Animal Behaviour*, *137*, 149–160. doi: 10.1016/j.anbehav.2017.12.019

Warren, J. M., & Warren, H. B. (1967). Spatial reversal learning by kittens. *Journal of Comparative and Physiological Psychology*, *63*(3), 523–525. doi: 10.1037/h0024627

Zentall, T. R. (2005). Selective and divided attention in animals. *Behavioural Processes*, *69*(1), 1–15. doi: 10.1016/j.beproc.2005.01.004

CHAPTER 4

The relationship between flight initiation distance and cognition of urban-living yellow mongoose, *Cynictis penicillata*



ABSTRACT

Behavioural changes are critical for animals to thrive in human-altered landscapes. Reduced flight initiation distance (FID) benefits urban-living animals by enabling them to forage in close proximity to humans. However, shorter FIDs require improved cognitive abilities, allowing them to assess the level of danger, and accordingly expend less energy by fleeing only when necessary. I assessed whether yellow mongooses, *Cynictis penicillata*, which are more tolerant to human disturbances, are also better problem-solvers. Yellow mongooses occurring in two locations, with distinct levels of human contact and varying proximities to human residents, were presented with a puzzle-box problem to solve for a food incentive (meat). I measured their responses to a non-threatening human approach, including FID (distance between observer and mongoose when flight is initiated), the distance fled from a puzzle box (distance from the box when mongoose terminated fleeing), the time taken to recover from the disturbance (time taken for mongoose to return to the puzzle box), and the problem-solving duration (latency to consume) following the human disturbance. The mongooses showed no difference in FID between locations but did have reduced FIDs at sites in closer proximity to human residents. Furthermore, mongooses in an area with greater human contact fled further away from the puzzle box, and took longer to recover from the human disturbance, than those in a more natural location with less human contact. Despite the differences in tolerance to human disturbance and the subsequent recovery, mongooses in the two locations displayed no difference in problem-solving efficiency. However, the mongooses' fear response and recovery time decreased in mongooses with lower tolerance to human disturbance, whereas problem-solving decreased in those that were more tolerant, possibly as a result of habituation to the human disturbance.
Keywords: *anthropogenic disturbance; cognition; FID; problem-solving; yellow mongoose*

INTRODUCTION

Urbanisation is driving behavioural changes in non-human animals (Sol et al., 2013). Urban expansion and the associated increase in human population density reduce the proximity between humans and wildlife, affecting animal population density, distribution, and behaviour (Palmer, 2003; Sol et al., 2013). Some of the behavioural adaptations of urban-living animals include a reduced fear response, a reduced stress response in the presence of humans and domestic animals, lower levels of aggression, and an increased tolerance to high population densities (Møller, 2009; Trut et al., 2009; Wirén et al., 2009). Furthermore,

several traits associated with urban-living animals benefit survival in these habitats, such as being innovative and bold (Møller, 2009). As a result, some animals are capable of living alongside the ever-increasing human population.

The distance at which an animal initiates flight from a potential threat, known as flight initiation distance (FID), is an indication of the perceived risk of predation by an individual, weighed against the cost of fleeing (Mikula, 2014). Not only does FID vary among different species (Blumstein et al., 2003), but also among individuals of the same species (e.g. McGowan et al., 2014). FID is thus a flexible behaviour (Mikula, 2014) and is modulated based on various factors such as the distance from the nearest refuge, the speed of the approaching threat, the physiological state of an individual, and previous experience (Engelhardt and Weladji, 2011). It further varies based on the level of human exposure in an animal's environment (Engelhardt and Weladji, 2011; McGowan et al., 2014; Mikula, 2014). The literature contains countless examples of the effects of increased human activity on animals' FIDs, specifically in areas with greater human activity where animals have shorter FIDs (e.g. birds: northern New Zealand dotterel, *Charadrius obscurus aquilonius*, Lord et al., 2001; Western gulls, *Larus occidentalis*, Webb and Blumstein, 2005; black-billed magpies, *Pica pica*, Kenney and Knight, 1992; reptiles: blue-tailed skinks, *Emoia impar*, McGowan et al., 2014; mammals: Cape ground squirrel, *Xerus inauris*, Chapman et al., 2012). This observation demonstrates the plastic nature of FIDs, indicating that learning plays a role in establishing FIDs (Eason et al., 2006; Mikula, 2014). Furthermore, there is evidence that variability in FID differs with habitat types, with individuals in an urban habitat reducing their FIDs, whereas the FIDs of those in non-urban areas remain constant (Møller et al., 2013), which indicates increased flexibility in FIDs in urban areas.

Flight initiation distance tends to increase with an individual's perceived predation risk as flight becomes more important than foraging or engaging in other activities that have an increased risk of predation (Bonenfant and Kramer, 1996; Cooper Jr., 1997). Ideally, animals should adjust their response based on the prevailing situation to minimise disturbance and maximise survival (Ydenberg and Dill, 1986; Bonenfant and Kramer, 1996) by assessing approaching danger and making a decision based on the perceived danger (Møller and Erritzøe, 2014). This method of cognitive monitoring reduces the relative cost of flights by selecting the least costly flights, rather than the fastest flights, in the presence of approaching danger (Møller and Erritzøe, 2014). It may further allow animals to distinguish between potentially threatening and nonthreatening approaches (Mikula, 2014), as well as distinguish between, and respond appropriately to, unfavourable (e.g. humans who are hostile towards

animals), neutral (e.g. humans who pay no attention to animals), and rewarding (e.g. humans who feed animals) stimuli, which may be crucial for survival (Belguermi et al., 2011; Goumas et al., 2020). Although longer FIDs may be beneficial in escaping danger early enough (Møller, 2014), they may not always outweigh the costs of fleeing, which include the loss of foraging opportunities and increased energy expenditure (Ydenberg and Dill, 1986). However, the ability to monitor the approaching danger, process the information, conduct a risk assessment, and act on this evaluation may be cognitively demanding (larger brain sizes are associated with shorter FIDs; Møller and Erritzøe, 2014). As a result, differences in cognitive abilities, personality, and prior encounters with humans may be essential for urban living (Goumas et al., 2020).

Shorter FIDs are especially important in urban habitats where animals coexist with humans (Møller et al., 2013). Having short FIDs is less likely to disrupt activities like foraging during frequent, non-threatening disturbances, reducing energy expenditure by fleeing less frequently, and reducing an animal's stress response (Møller et al., 2013). However, urbanisation may change an animal's risk assessment. In urban areas, where human presence is inevitable, animals are expected to display decreased sensitivity to humans, possibly as a result of habituation (Kenney and Knight, 1992; Webb and Blumstein, 2005). However, some animals may become habituated, whereas others may fail to habituate or even become sensitised to humans (Blumstein et al., 2003; Goumas et al., 2020), even if the human-animal interaction is not negative (McGowan et al., 2014). For example, Magellanic penguins, *Spheniscus magellanicus*, appear to habituate to humans through a reduced stress response when exposed to humans (Walker et al., 2006), whereas yellow-eyed penguins, *Megadyptes antipodes*, become sensitised and have an increased stress response when exposed to humans (Ellenberg et al., 2007), compared with their unexposed conspecifics. A better understanding of the adaptations of animals in urban environments is, therefore, crucial in reducing the impacts of urbanisation on wildlife.

Many behavioural characteristics of animals adapted to the presence of humans are also predictors of innovation, cognition, and problem-solving success. It is for this reason that urban-living animals often display enhanced problem-solving abilities (e.g. Mazza and Guenther, 2021). Some of these characteristics include reduced neophobia (e.g. Bergman and Kitchen, 2009; Biondi et al., 2010; Daniels et al., 2019), the ability to learn (e.g. Thornton and Samson, 2012), and larger brain size (Reader and Laland, 2002), all of which have been suggested to influence animals' fear responses to humans (Eason et al., 2006; Møller and Erritzøe, 2014; Goumas et al., 2020). But, are animals with increased tolerance of humans

better at problem-solving, following a human disturbance, than those that are more sensitive to humans? If so, these two factors, tolerance to humans and improved problem-solving, may function together to support an animal's ability to thrive in urban habitats. Yet, the research that is presently lacking is the impact of direct human disturbance on the behaviour and cognitive abilities of urban-living animals, as well as the cognitive mechanisms underlying these behavioural responses (Goumas et al., 2020).

My study involved urban-living yellow mongooses, *Cynictis penicillata*. The yellow mongoose is a small (length: 300 mm, weight: 500 – 1000 g; Kingdon et al., 2013) carnivore distributed throughout southern Africa (Do Linh San et al., 2015). It is diurnal and most active in the mornings between 06h00 and 12h00 (Cronk and Pillay, 2019a, 2020). This species has a history of persecution by humans since it is considered a pest on farms (Lynch, 1980) and a carrier of rabies disease (Bishop, 2010). Even so, it has managed to become well-established in urban areas where it lives alongside humans and exploits anthropogenic food (Cronk and Pillay, 2018, 2019a, 2019b). Therefore, the appropriate behavioural responses that involve exploiting the available resources, yet avoiding humans in this human-altered landscape, may be essential for its survival (Goumas et al., 2020).

In a previous experiment (Chapter 2), I showed that the level of disturbance in the environment of urban yellow mongooses might affect their problem-solving ability (problem-solving differed among three urban locations, possibly due to varying levels of human disturbance). A more direct approach to assess the effects of human disturbance on problem-solving ability may be to relate the response of individual yellow mongooses to human disturbance (and their subsequent stress response and recovery) to their problem-solving efficiency. In this study, I measured the FID and problem-solving efficiency in yellow mongooses at sites with varying levels of human activity to assess the direct effect of human disturbance on problem-solving ability.

The aim of this study was to assess how the direct disturbance by human presence affects yellow mongooses' cognition in an urban habitat. I assessed the level of tolerance mongooses have to human disturbance during a puzzle box problem-solving task. I predicted that mongooses in areas of high human presence would be more tolerant of human disturbances by (i) having a shorter flight initiation distance, and (ii) fleeing a shorter distance from the box when approached by a person compared with mongooses in areas of lower human presence. I also assessed the recovery rate following a human disturbance and predicted that mongooses in areas of high human presence would recover quicker following a disturbance than those in areas of lower human presence. I further assessed the relationship

between the tolerance to human disturbance, and subsequent recovery thereafter, as well as the problem-solving ability of yellow mongooses, and predicted that mongooses that are able to recover quickly from a human disturbance would be better at solving a puzzle box problem following a human disturbance. Finally, I established whether habituation to the human disturbance would influence the tolerance, recovery, and problem-solving ability of mongooses, and predicted that the (i) FID, (ii) distance fled, (iii) recovery rate, and (iv) latency to consume would decrease over successive trials as mongooses become habituated to humans.

MATERIALS AND METHODS

Study area

This study was conducted in the Meyersdal area situated in the south of Johannesburg, South Africa. Two areas were selected for study, the Meyersdal Nature Estate (26°18’08.2”S 28°04’55.9”E; 300 ha) and the Meyersdal Eco Estate (26°17’03.6”S 28°04’50.8”E; 480 ha). These locations were adjacent to one another but separated by a double-laned tar road which the mongooses in this area rarely crossed (Cronk and Pillay, 2021). The Nature Estate had a nature area that was fenced off from the residential area, with low levels of interaction between human residents and wildlife, although it was occasionally accessed by human hikers, runners, and cyclists. The Eco Estate had no separate nature area, and instead, the residences were dispersed throughout a nature area resulting in increased interaction between the residents and wildlife. A total of five sites were selected for this study based on the occurrence of yellow mongooses, and a distance of at least 200 m from any other site. Three of these sites were in the Nature Estate, and two were in the Eco Estate. Only five sites were viable for conducting this experiment due to mongooses’ generally cryptic behaviour and reluctance to emerge from their burrows in the presence of humans. The sites used in this study were the only sites where mongooses were frequently present during the experimental set-up and engaged with the puzzle box in my presence.

Experimental design and protocol

The yellow mongoose is diurnal, and accordingly, this experiment was conducted between 6h00 and 12h00 daily when the mongooses were the most active (Cronk and Pillay, 2019a, 2020). For this experiment, mongooses were exposed to puzzle boxes constructed of

clear Perspex with a lid that could open and close with hinges. Meat offcuts (1 teaspoon) were placed inside the box as an incentive to solve the puzzle box problem. This study took place between May and July 2021. As a result of the time elapsed since mongooses solved the puzzle box problem during the previous experiment, as well as two sites that were not used previously (Chapter 3), the mongooses were trained to open the puzzle boxes at all sites. This included two stages: stage 1, where the mongooses were exposed to a puzzle box with an open lid allowing for habituation, and stage 2, where mongooses were exposed to a puzzle box with a mostly closed lid propped up with a stick, leaving a 1 cm opening. The mongooses had to obtain the food incentive from the puzzle box successfully for a total of five trials at stage 1 before proceeding to stage 2. After the mongooses successfully obtained the food incentive from the puzzle box at stage 2 for a total of five trials, the lids of the puzzle boxes were closed entirely, and the experiment commenced.

The puzzle box with the closed lid containing the food incentive was either placed near the den entrance or in a location near the dens that mongooses were observed visiting frequently. A human observer (kept constant during all trials and at all sites) remained at approximately 10 – 20 m from the puzzle box (at two sites, the mongooses were tolerant of human observers at a distance of 10 m from the box, whereas at the remaining three sites, mongooses only emerged from their dens when human observers were 20 m away). Once a mongoose contacted the box, the human observer approached the box at a slow pace and in a non-threatening manner. The location of the human observer at the exact moment the mongoose fled from the box was marked by laying a placeholder on the ground. Once the mongoose stopped fleeing, the location of the mongoose was marked visually by a second observer (kept constant during all trials and at all sites) who remained at the starting position. After the mongoose stopped fleeing, the first observer slowly retreated to the starting position. The recovery time was recorded as the time (in seconds) that elapsed from when the mongoose fled from the box to when it contacted the box again. Whenever the mongoose did not return to the puzzle box for over 10 min, the trial was terminated, and the recovery time was recorded as 600 s (i.e. the maximum time). The latency to consume the food incentive, which indicated problem-solving efficiency, was recorded as the time elapsed from when the mongoose contacted the box until it solved the problem and consumed the food after returning to the puzzle box. After the mongoose had consumed the food incentive and abandoned the puzzle box, the distance between the first marker and the puzzle box, as well as the puzzle box and the second marker, were measured (in metres) using a measuring tape. The first measurement indicated flight initiation distance (FID), and the second indicated the

distance fled. The experiment was repeated at each site for a total of five trials per site. Sampling for FID experiments were opportunistic since the presence of the same focal mongoose at the puzzle box in the presence of the observer occurred infrequently. Five was therefore the maximum number of trials possible without mongooses being absent during the experimental set-up for several consecutive days, possibly impacting the results. The straight-line distance between the site and the nearest human residents was measured using Google Earth™ and used as a measure of the effect of human resident proximity on the yellow mongooses' FID, distance fled, recovery rate, and latency to consume.

Because yellow mongooses are predominantly solitary foragers (le Roux et al., 2008; Manser et al., 2014), the same focal individual consistently visited the puzzle box (confirmed using facial recognition technology; School of Computational and Applied Mathematics, University of the Witwatersrand). Only adult mongooses participated in this study, and juveniles never attempted to solve the puzzle box problem. Males and females could not be distinguished due to yellow mongooses' lack of sexual dimorphism, and therefore sex was not considered in this study. Furthermore, the Meyersdal management did not approve the collaring or marking of individuals in this study.

Data analyses

All statistical analyses were conducted using R Statistical Software (R version 3.4.3; R Core Team, 2013; http://www.R-project.org/). Shapiro-Wilk tests were used to test for normality. Non-normal variables were transformed using a Box-Cox transformation (R package: MASS). Flight initiation distance (FID) was adjusted as a ratio of the starting distance by dividing the FID by the starting distance, to account for the variation in starting distance among sites. A linear mixed effect model (LMER; R packages: lme4, lmerTest) was used to analyse differences in (i) the flight initiation distance (FID), (ii) distance fled, (iii) recovery time, and (iv) latency to consume. Location was a fixed effect, site and trial were random factors, and proximity to the nearest human residents was a covariate. When proximity to the nearest human residents was significant, a Pearson's product-moment correlation was used to assess the relationship between the relevant response variable (FID, distance fled, recovery time, latency to consume) and the proximity to the nearest human residents. Effect sizes were evaluated using Cohen's D (R package: EMAtools). Linear models were used to assess whether (i) FID, (ii) distance fled, and (iii) recovery rate influenced the latency to consume the food incentive.

Ethical approval

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2021/06/03/B).

RESULTS

For the flight initiation distance experiments, five active sites were identified and used (three sites in the Nature Estate and two sites in the Eco Estate). At three sites, two in the Eco Estate and one in the Nature Estate, mongooses were reluctant to emerge from their refuge and approach the puzzle box with the human observer 10 m away from the puzzle box. At these sites, the starting distance of the human observer was increased to 20 m whilst keeping the starting distance constant at 10 m at the remaining two sites. The mongooses in this experiment rarely fled to the nearest refuge (28% of all trials) and mostly stopped fleeing while still in sight of the observer. Further, except for one trial, mongooses always recovered from the human disturbance before returning to the puzzle box to obtain the food incentive. During the one trial where the mongoose did not return to the puzzle box within the 10-minute limit, the recovery rate was recorded as 600 s. Despite the small sample size in this study, the difference between means was sufficiently large, as indicated by the large effect size (Cohen's D) for significant results.

Flight initiation distance (FID)

Location ($\chi^2 = 25.83$, df = 1, $p < 0.001$; LMER; Cohen's D = -6.08; Figure 1a) and the proximity to the nearest human residents ($\chi^2 = 31.66$, df = 1, $p < 0.001$; Cohen's D = 6.74; Figure 1b) were significant predictors of the flight initiation distance (FID). The flight initiation distance (m), when adjusted for the starting point of the human observer (10 m vs 20 m), was significantly longer in the Meyersdal Eco Estate compared with the Meyersdal Nature Estate (Figure 1a). There was a positive, significant relationship between the flight initiation distance (m) and the distance to human residents ($r_p = 0.42$, $p = 0.035$; Pearson's product-moment correlation; Figure 1b). Flight initiation distance increased with increased distance the nearest human residents.

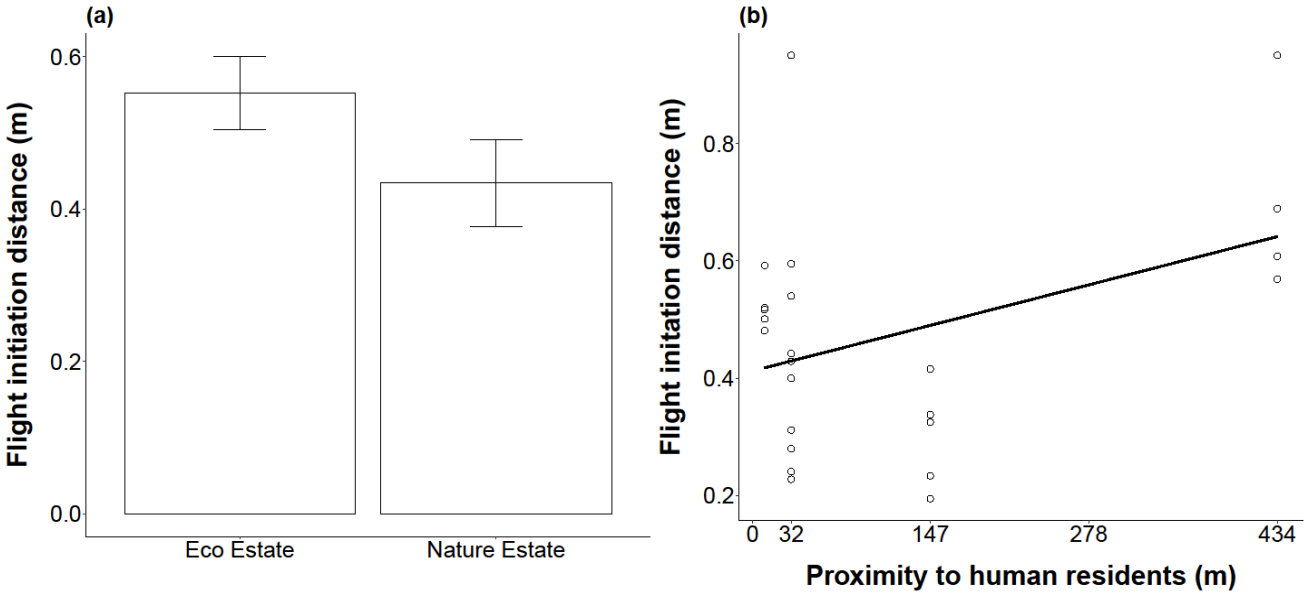


Figure 1. (a) The mean flight initiation distance (m) during puzzle box experiments at the Meyersdal Eco Estate and Meyersdal Nature Estate. Error bars indicate standard error. **(b)** The relationship between the adjusted flight initiation distance (m) and distance to human residents (m). The trend line is significant (p = 0.035; Pearson's product-moment correlation).

A change in FID over trials would have indicated that mongooses changed their FID as they became habituated to the human disturbance. However, the FID did not change in any particular direction over the five trials (Figure 2).

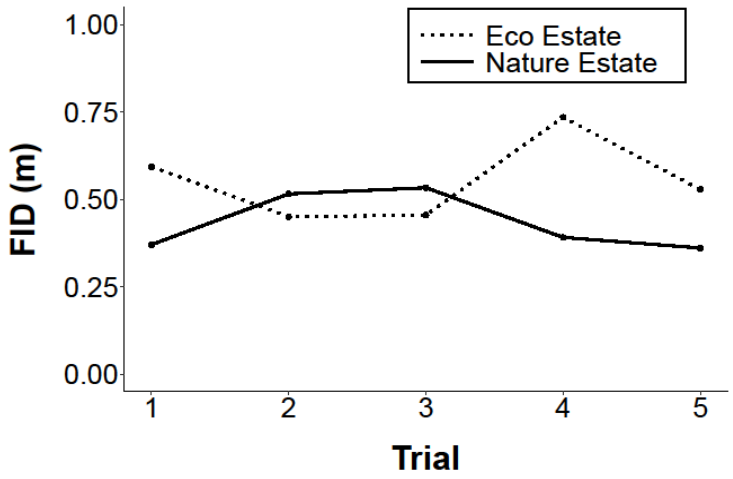


Figure 2. The change in mean flight initiation distance (FID) of yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during FID experiments. The FIDs are adjusted for starting distance.

Distance fled

Location (χ^2 = 13.53, df = 1, p < 0.001; LMER; Cohen's D = -3.30; Figure 3) was a significant predictor of the distance fled, but the proximity to human residents was not (χ^2 =

0.01, df = 1, p = 0.910; Cohen's D = -0.10). The distance fled from the puzzle box was significantly longer in the Meyersdal Eco Estate compared with the Meyersdal Nature Estate (Figure 3).

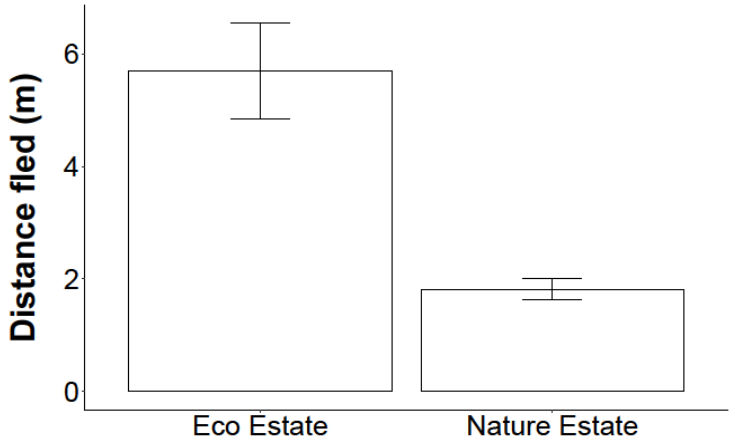


Figure 3. The mean distance yellow mongooses fled from the puzzle box during flight initiation (FID) experiments at the Meyersdal Eco Estate and Meyersdal Nature Estate. Error bars indicate standard error.

A decrease in the distance fled over trials would have indicated that mongooses adjusted their response as they became used to the human disturbance. The distance fled from the box decreased over trials in both locations, especially after the first trial, with the spike at trial 4 in the Eco Estate probably anomalous (Figure 4).

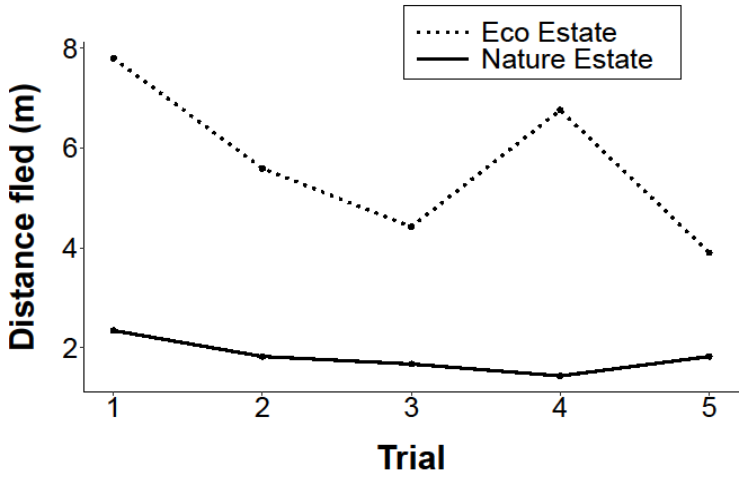


Figure 4. The change in mean distance fled (m) of yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during flight initiation distance (FID) experiments.

Recovery rate

The recovery rate was measured as the time elapsed since a mongoose terminated fleeing until it returned to the puzzle box. This was a measure of the rate at which a mongoose was able to recover from human disturbance and return to the place of the initial disturbance. Location was a significant predictor of the recovery rate ($\chi^2 = 13.48$, df = 1, $p < 0.001$; Cohen's D = -5.19; Figure 5), whereas proximity to the nearest human residents was not a significant predictor of the recovery rate ($\chi^2 = 1.85$, df = 1, $p = 0.174$; Cohen's D = 1.92). The recovery rate was significantly longer in the Eco Estate compared with the Nature Estate.



Figure 5. The mean recovery rate (s) after yellow mongooses fled from the puzzle box during flight initiation (FID) experiments at the Meyersdal Eco Estate and Meyersdal Nature Estate. Error bars indicate standard error.

A decrease in the recovery rate over trials would have indicated that mongooses were able to recover faster following a human disturbance as they became used to the disturbance. The recovery rate decreased over the five trials in the Eco Estate, especially after the first trial, with an increase at trials 4 and 5, and no considerable change in recovery rate over the five trials in the Nature Estate (Figure 6).

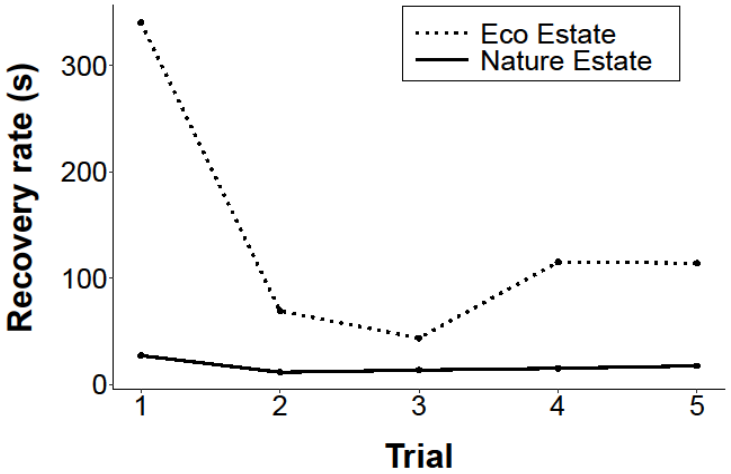


Figure 6. The change in mean recovery rate (s) of yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during flight initiation distance (FID) experiments.

Latency to consume

The latency to consume the food incentive was a measure of mongooses' problem-solving efficiency after being exposed to, and having recovered from, a human disturbance. Location ($\chi^2 = 0.60$, df = 1, p = 0.440; Cohen's D = 0.34) and the proximity to the nearest human residents ($\chi^2 = 0.01$, df = 1, p = 0.917; Cohen's D = -0.05) did not significantly predict the latency to consume the food incentive. Furthermore, linear models revealed that the latency to consume was not influenced by the FID (t = -0.33, p = 0.747), the distance fled (t = -1.53, p = 0.141), or the recovery rate (t = -1.34, p = 0.193).

A decrease in the latency to consume the food incentive over trials would have indicated that the mongooses had improved efficiency at solving the puzzle box problem as they became used to the human disturbance. The latency to consume the food increased after the first trial in the Eco Estate and decreased after the first trial in the Nature Estate (Figure 7).

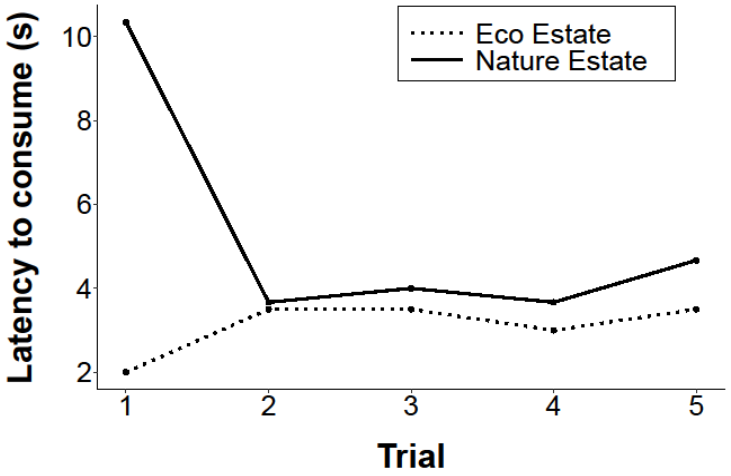


Figure 7. The change in mean latency to consume (s) a food incentive by yellow mongooses over five trials in the Meyersdal Eco Estate and Meyersdal Nature Estate in response to an approaching human observer during flight initiation distance (FID) experiments.

DISCUSSION

I conducted flight initiation distance (FID) experiments to assess the impact of direct human disturbance on the problem-solving abilities of an urban population of yellow mongooses. The mongooses in my study showed significant differences in their tolerance to human disturbance based on their location. Mongooses in areas with greater human disturbance had longer flight initiation distances than those in a more natural habitat with reduced human presence. Conversely, mongooses occurring further away from human residents had longer flight initiation distances than those in close proximity to human residents. In addition, the mongooses in areas with greater human disturbance fled further away from the puzzle box, and took longer to recover following a human disturbance, than those in a more natural area. Although mongooses had different levels of tolerance to direct human disturbance based on their locality, the mongooses showed no difference in problem-solving efficiency following the disturbance. Moreover, mongooses' problem-solving efficiency was not predicted by their FID, distance fled, or recovery rate, but still changed over the various trials.

The mongooses in the Eco Estate spent less time engaging with the puzzle box problem before fleeing from an approaching human, and therefore had longer FIDs compared with those in the Nature Estate, which remained at the box until the human observer was much closer. This is contrary to my prediction and the literature, which suggests that animals in areas of greater human density have shorter FIDs (e.g. Lord et al., 2001; Webb and Blumstein, 2005; Chapman et al., 2012; Møller et al., 2013; McGowan et al., 2014). Interestingly, the FIDs of mongooses decreased with increased proximity to human residents, which, in fact, supports both my prediction and the literature. The differences in FID between

the two locations must, therefore, be unrelated to human presence and more likely the result of other differences between the two locations. There are numerous potential reasons for this observed difference in FID, including naivety in areas with reduced human contact, familiarity with the human observer, previous experience, response to novelty, the presence of domestic animals, the effects of indirect disturbances, and food availability. Although it is not possible to determine which one of these factors, or possibly a combination of factors, caused this disparity in FID between the two locations, each one will be discussed briefly below.

The first possible explanation for the differences in FID between the two locations in this study is the naivety of animals occurring in areas with low levels of human encounters. Naivety of animals towards predators is a common phenomenon (e.g. on islands) when native animals are isolated from alien predators, resulting in inappropriate antipredator responses in the presence of introduced predators (naïve prey hypothesis; Sih et al., 2010). Similarly, when human encounters are rare or non-existent, animals may not exhibit the usual fear responses in the presence of humans (e.g. Galapagos Islands' marine iguanas, *Amblyrhynchus cristatus*, Vitousek et al., 2010). Mongooses in the Eco Estate, where residents live in the nature area, likely encountered humans daily, resulting in a greater fear response compared with those in the Nature Estate, which rarely encountered humans and, accordingly, do not show such a fear response. This seems to be the least likely explanation for the observed difference in FID since mongooses in the Nature Estate encountered humans occasionally and are likely to be moderately familiar with humans. If, however, animals have encountered humans before, habituation can occur over time, leading to a reduced fear response. For animals to habituate to humans, they must be able to categorise all humans as one group (Goumas et al., 2020). In this case, an encounter with one human may influence an animal's reaction to another human as a result of experience (Belguermi et al., 2011; Goumas et al., 2020). Additionally, for animals to habituate only to certain humans that are rewarding, and sensitise to certain humans that are dangerous, they must have the ability to distinguish between different humans (Goumas et al., 2020), which many species of animals are capable of (e.g. wild jackdaws, *Corvus monedula,* Davidson et al., 2015; feral pigeons, *Columba livia*, Belguermi et al., 2011; house sparrows, *Passer domesticus*, Vincze et al., 2015; honeybees, *Apis mellifera*, Dyer et al., 2005; sheep, *Ovis aries*, Knolle et al., 2017). This ability to discriminate between dangerous, neutral, and rewarding humans may be advantageous when living in close proximity to humans (Belguermi et al., 2011; Goumas et al., 2020), especially since fleeing during a non-threatening approach is costly (Ydenberg and

Dill, 1986). The mongooses in the Nature Estate were often already present or emerged from their dens during the set-up of various experiments by the same human observer and may have learned to recognise the observer as non-threatening, thereby reducing their fear response. This is in direct contrast to the mongooses in the Eco Estate who were rarely present during experimental set-up and never had the opportunity to associate the observer with any reward or recognise them as non-threatening. Additionally, the mongooses in the Eco Estate may have had negative encounters with humans previously, or lacked the ability to discriminate between threatening and non-threatening humans, and consequently responded to the observer's approach based on prior experience (some urban animals fail to adapt their behavioural responses to threatening and non-threatening humans in areas with high human population densities; Vincze et al., 2015). Similarly, the mongooses in the Nature Estate may have had positive experiences with humans previously and subsequently were attracted to the human observer (e.g. Sabbatini et al., 2006) due to prior associations between humans and food rewards.

Differences in response to novelty (neophobia/neophilia) may impact animals' general processing of cues in their environment and, as a result, may influence their response to humans (Greggor et al., 2019; Goumas et al., 2020). In a previous experiment conducted on the same population of mongooses, those occurring in the Eco Estate were initially more neophobic when presented with a novel object (Chapter 2). Their increased neophobia, generally, may have resulted in an increased sensitivity and fear response towards humans. Further, animals' fear responses to humans may be influenced by the predation risk in their environment (Goumas et al., 2020), promoting antipredator responses towards humans. For example, double-banded plovers, *Charadrius bicinctus*, have longer FIDs in areas with more domestic animals (St Clair et al., 2010). Domestic animals were prohibited from entering the fenced-off area in which mongoose sites were located in the Nature Estate, with the complete prohibition of domestic cats in the estate, whereas both dogs on-leash and free-roaming cats occurred in the Eco Estate. This increased exposure to domestic animals in the Eco Estate may have increased mongooses' sensitivity to predation overall, raising antipredator responses to humans in general.

There are various ways in which altered habitats affect animals. Indirect effects, for example, vehicular traffic, noise pollution, and domestic animals (McGowan et al., 2014), should be considered in combination with the direct effects of human presence. This is because these indirect effects alter the way in which animals behave and perceive risk, and it may limit their ability to acquire resources (Gill, 2007). Observed changes in FID may thus

be the result of indirect disturbances altering the perceived risk of predation, and not necessarily the direct impact of human presence exclusively (Li et al., 2011). Since the Eco Estate is mostly residential and developed (e.g. presence of tar roads, vehicles, domestic animals, and noise from residents), mongooses here likely encountered indirect disturbances much more frequently than the mongooses in the Nature Estate did, possibly increasing their sensitivity to human presence. The FID of an animal may also decrease with food availability since reduced food availability will increase an animal's motivation to feed (Fernández-Juricic et al., 2002). The mongooses in the Eco Estate may have acquired food elsewhere and were not as motivated to feed as the mongooses in the Nature Estate, and, therefore, had longer FIDs.

The FIDs did not decrease over the five trials as expected. Instead, it remained constant, with the first and last trials having similar FIDs in both locations. This indicates that mongooses did not adjust their FIDs even when they became habituated to the human disturbance (as indicated by the reduced fear response via distance fled and recovery rate over the five trials) in both locations. After conducting an FID experiment on birds across Europe, Møller et al. (2013) disputed that differences in FID between different environments result from phenotypic plasticity, especially since individual animals tend to have consistent FIDs across different habitats (Møller and Garamszegi, 2012). The results from my study also did not support habituation as a driver of variations in FID between the two locations since, if that were the case, those in areas with greater human density would have exhibited shorter FIDs (Møller et al., 2013). Phenotypic sorting, the distribution of individuals among environments that best suit their specific FIDs (Carrete and Tella, 2010), was also considered an unlikely explanation due to the high genetic variation in urban populations as well as their reduced dispersal ranges (Björklund et al., 2009; Møller et al., 2013; O'Donnell and delBarco-Trillo, 2020). Thus, the most likely explanation was that urban individuals with long FIDs have higher mortality rates due to the costs associated with frequent flights (e.g. reduced foraging time and high energy expenditure; Ydenberg and Dill, 1986), resulting in microevolutionary changes (Hendry et al., 2008; Møller et al., 2013). In this way, each location may have selected for the optimal FID based on the environmental pressures. An interesting future study would be a non-urban, urban comparison to establish whether the FIDs of the mongooses in the Eco Estate are significantly shorter, indicating variation in the reduction of FIDs based on environmental pressures in various urban areas.

When taken together, the FID, distance fled, and recovery rate results suggest that the mongooses in the Eco Estate were less tolerant of human disturbances than those in the

Nature Estate. Based on these findings, I predicted that mongooses in the Eco Estate would be slower at solving the puzzle box problem than those in the Nature Estate due to their reduced tolerance to human disturbance. However, the mongooses were equally efficient in solving the puzzle box problem in both estates, irrespective of their FID, distance fled, and recovery rate. This suggests that direct human disturbance did not affect the problem-solving ability of urban-dwelling yellow mongooses in my study. The mongooses' problem-solving ability changed over the five trials, with those in the Eco Estate becoming less efficient, and those in the Nature Estate becoming more efficient, after the first trial. Thus, although a human disturbance did not affect the mongooses' problem-solving, the eventual habituation to the disturbance did improve problem-solving efficiency in mongooses with greater tolerance to human disturbance, whereas the problem-solving efficiency worsened in mongooses with a lower level of tolerance during frequent disturbances by humans. It is possible that the behaviour of the two mongooses investigated in the Eco Estate was anomalous and differed from the rest of the population, which would have impacted the results observed. Increasing the sample size by including additional sites in future studies would be beneficial to ensure that the observations made are representative of all individuals within a specific location.

The mongooses in my study had distinct fear responses to humans based on their location, with those in areas of increased human disturbance fleeing earlier during a human disturbance, fleeing further away from the site of the disturbance, and taking longer to recover from the disturbance than those in a more natural habitat with less human disturbance. Even so, the mongooses showed adaptation to the level of disturbance, as demonstrated by their shorter FIDs in closer proximity to human residents. Furthermore, their FIDs were consistent over time even though the distance fled from the disturbance and the time to recover decreased, indicating that mongooses became used to the human disturbance but did not alter their initial fear response accordingly. Notably, their problem-solving abilities were not associated with direct human disturbances, but the ability to adapt to these disturbances may have affected their problem-solving efficiency. Problem-solving efficiency may be more closely linked to tolerance to human disturbance than previously thought, with reduced problem-solving efficiency in mongooses with lower levels of tolerance to humans, even after improved recovery from direct disturbances. Together, adaptation to human disturbances may benefit survival in urban settings by promoting foraging opportunities through shorter FID and improved problem-solving when obtaining a food incentive.

REFERENCES

Belguermi, A., Bovet, D., Pascal, A., Prévot-Julliard, A.-C., Saint Jalme, M., Rat-Fischer, L., & Leboucher, G. (2011). Pigeons discriminate between human feeders. *Animal Cognition*, *14*(6), 909–914. doi: 10.1007/s10071-011-0420-7

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). *Animal Cognition*, *12*(1), 63–73. doi: 10.1007/s10071-008-0171-2

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal Cognition*, *13*(5), 701–710. doi: 10.1007/s10071-010-0319-8

Bishop, G. C. (2010). *Rabies: Guide for the medical, veterinary and allied professions* (2nd ed). Pretoria: Dept. of Agriculture, Forestry and Fisheries.

Björklund, M., Ruiz, I., & Senar, J. C. (2009). Genetic differentiation in the urban habitat: The great tits (*Parus major*) of the parks of Barcelona city. *Biological Journal of the Linnean Society*, *99*(1), 9–19. doi: 10.1111/j.1095-8312.2009.01335.x

Blumstein, D. T., Anthony, L. L., Harcourt, R., & Ross, G. (2003). Testing a key assumption of wildlife buffer zones: Is flight initiation distance a species-specific trait? *Biological Conservation*, *110*(1), 97–100. doi: 10.1016/S0006-3207(02)00180-5

Bonenfant, M., & Kramer, D. L. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behavioral Ecology*, *7*(3), 299–303. doi: 10.1093/beheco/7.3.299

Carrete, M., & Tella, J. L. (2010). Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. *Biology Letters*, *6*(2), 167–170. doi: 10.1098/rsbl.2009.0739

Chapman, T., Rymer, T., & Pillay, N. (2012). Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris*. *Naturwissenschaften*, *99*(11), 893–902. doi: 10.1007/s00114-012-0971-8

Cooper Jr., W. E. (1997). Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology*, *75*(6), 943–947. doi: 10.1139/z97-113

Cronk, N. E., & Pillay, N. (2018). Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethologica*, *21*(2), 127–136. doi: 10.1007/s10211-018-0291-x

Cronk, N. E., & Pillay, N. (2019a). Flexible Use of Urban Resources by the Yellow Mongoose *Cynictis penicillata*. *Animals*, *9*(7), 447. doi: 10.3390/ani9070447

Cronk, N. E., & Pillay, N. (2020). Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment. *Journal of Urban Ecology*, *6*(1), 1–9. doi: 10.1093/jue/juaa013

Cronk, N. E., & Pillay, N. (2021). Home range and use of residential gardens by yellow mongoose *Cynictis penicillata* in an urban environment. *Urban Ecosystems*, *24*(1), 127–139. doi: 10.1007/s11252-020-01022-1

Cronk, N., & Pillay, N. (2019b). Dietary overlap of two sympatric African mongoose species in an urban environment. *Mammalia*, *85*(5), 428–438. doi: 10.1515/mammalia-2018-0113

Daniels, S. E., Fanelli, R. E., Gilbert, A., & Benson-Amram, S. (2019). Behavioral flexibility of a generalist carnivore. *Animal Cognition*, *22*(3). doi: 10.1007/s10071-019-01252-7

Davidson, G. L., Clayton, N. S., & Thornton, A. (2015). Wild jackdaws, *Corvus monedula*, recognize individual humans and may respond to gaze direction with defensive behaviour. *Animal Behaviour*, *108*, 17–24. doi: 10.1016/j.anbehav.2015.07.010

Do Linh San, E., Cavallini, P., & Taylor, P. (2015). *The IUCN Red List of Threatened Species 2015* [Data set]. International Union for Conservation of Nature. doi: 10.2305/IUCN.UK.2015-4.RLTS.T41597A45205726.en

Dyer, A. G., Neumeyer, C., & Chittka, L. (2005). Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. *Journal of Experimental Biology*, *208*(24), 4709–4714. doi: 10.1242/jeb.01929

Eason, P. K., Sherman, P. T., Rankin, O., & Coleman, B. (2006). Factors affecting flight initiation distance in American robins. *Journal of Wildlife Management*, *70*(6), 1796–1800. doi: 10.2193/0022-541X(2006)70[1796:FAFIDI]2.0.CO;2

Ellenberg, U., Setiawan, A. N., Cree, A., Houston, D. M., & Seddon, P. J. (2007). Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins

exposed to unregulated tourism. *General and Comparative Endocrinology*, *152*(1), 54–63. doi: 10.1016/j.ygcen.2007.02.022

Engelhardt, S. C., & Weladji, R. B. (2011). Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Canadian Journal of Zoology*, *89*(9), 823–830. doi: 10.1139/z11-054

Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, *80*(7), 1212–1220. doi: 10.1139/z02-104

Gill, J. A. (2007). Approaches to measuring the effects of human disturbance on birds: Measuring the effects of human disturbance on birds. *Ibis*, *149*, 9–14. doi: 10.1111/j.1474-919X.2007.00642.x

Goumas, M., Lee, V. E., Boogert, N. J., Kelley, L. A., & Thornton, A. (2020). The role of animal cognition in human-wildlife interactions. *Frontiers in Psychology*, *11*, 589978. doi: 10.3389/fpsyg.2020.589978

Greggor, A. L., Trimmer, P. C., Barrett, B. J., & Sih, A. (2019). Challenges of learning to escape evolutionary traps. *Frontiers in Ecology and Evolution*, *7*, 408. doi: 10.3389/fevo.2019.00408

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*(1), 20–29. doi: 10.1111/j.1365-294X.2007.03428.x

Kenney, S. P., & Knight, R. L. (1992). Flight distances of black-billed magpies in different regimes of human density and persecution. *The Condor*, *94*(2), 545–547. doi: 10.2307/1369231

Kingdon, J., Happold, D., Butynski, T., Hoffman, M., Happold, M., & Kalina, J. (Eds.). (2013). *Cynictis penicillata*, Yellow Mongoose. In *Mammals of Africa. Vol. 5: Carnivores, pangolins, equids and rhinoceroses* (pp. 334–339). London: Bloomsbury.

Knolle, F., Goncalves, R. P., & Morton, A. J. (2017). Sheep recognize familiar and unfamiliar human faces from two-dimensional images. *Royal Society Open Science*, *4*(11), 171228. doi: 10.1098/rsos.171228

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behaviour*, *75*(3), 943–949. doi: 10.1016/j.anbehav.2007.07.014

Li, C., Monclús, R., Maul, T. L., Jiang, Z., & Blumstein, D. T. (2011). Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. *Applied Animal Behaviour Science*, *129*(2–4), 146–152. doi: 10.1016/j.applanim.2010.11.013

Lord, A., Waas, J. R., Innes, J., & Whittingham, M. J. (2001). Effects of human approaches to nests of northern New Zealand dotterels. *Biological Conservation*, *98*(2), 233–240. doi: 10.1016/S0006-3207(00)00158-0

Lynch, C. D. (1980). *Ecology of the suricate, Suricata suricatta, and yellow mongoose, Cynictis penicillata, with special reference to their reproduction*. Bloemfontein, Republiek van Suid-Afrika: Nasionale Museum.

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal Complexity in Meerkats and Other Mongoose Species. *Advances in the Study of Behavior*, *46*, 281–310. doi: 10.1016/B978-0-12-800286-5.00006-7

Mazza, V., & Guenther, A. (2021). City mice and country mice: Innovative problem solving in rural and urban noncommensal rodents. *Animal Behaviour*, *172*, 197–210. doi: 10.1016/j.anbehav.2020.12.007

McGowan, M. M., Patel, P. D., Stroh, J. D., & Blumstein, D. T. (2014). The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. *Ethology*, *120*(11), 1081–1089. doi: 10.1111/eth.12281

Mikula, P. (2014). Pedestrian density influences flight distances of urban birds. *Ardea*, *102*(1), 53–60. doi: 10.5253/078.102.0105

Møller, A. P. (2009). Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, *159*(4), 849–858. doi: 10.1007/s00442-008-1259-8

Møller, A. P. (2014). Life history, predation and flight initiation distance in a migratory bird. *Journal of Evolutionary Biology*, *27*(6), 1105–1113. doi: 10.1111/jeb.12399

Møller, A. P., & Erritzøe, J. (2014). Predator-prey interactions, flight initiation distance and brain size. *Journal of Evolutionary Biology*, *27*(1), 34–42. doi: 10.1111/jeb.12272

Møller, A. P., & Garamszegi, L. Z. (2012). Between individual variation in risk-taking behavior and its life history consequences. *Behavioral Ecology*, *23*(4), 843–853. doi: 10.1093/beheco/ars040

Møller, A. P., Grim, T., Ibanez-Alamo, J. D., Marko, G., & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, *24*(5), 1211–1217. doi: 10.1093/beheco/art054

O'Donnell, K., & delBarco-Trillo, J. (2020). Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: A meta-analysis. *Journal of Urban Ecology*, *6*(1), juaa014. doi: 10.1093/jue/juaa014

Palmer, C. (2003). Colonization, urbanization, and animals. *Philosophy & Geography*, *6*(1), 47–58. doi: 10.1080/1090377032000063315

R Core Team. (2013). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.R-project.org/

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*(7), 4436–4441. doi: 10.1073/pnas.062041299

Sabbatini, G., Stammati, M., Tavares, M. C. H., Giuliani, M. V., & Visalberghi, E. (2006). Interactions between humans and capuchin monkeys (*Cebus libidinosus*) in the Parque Nacional de Brasília, Brazil. *Applied Animal Behaviour Science*, *97*(2–4), 272–283. doi: 10.1016/j.applanim.2005.07.002

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., … Vonesh, J. R. (2010). Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, *119*(4), 610–621. doi: 10.1111/j.1600-0706.2009.18039.x

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

St Clair, J. J. H., García-Peña, G. E., Woods, R. W., & Székely, T. (2010). Presence of mammalian predators decreases tolerance to human disturbance in a breeding shorebird. *Behavioral Ecology*, *21*(6), 1285–1292. doi: 10.1093/beheco/arq144

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468. doi: 10.1016/j.anbehav.2012.03.018

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: The domesticated fox as a model. *BioEssays*, *31*(3), 349–360. doi: 10.1002/bies.200800070

Vincze, E., Papp, S., Preiszner, B., Seress, G., Liker, A., & Bókony, V. (2015). Does urbanization facilitate individual recognition of humans by house sparrows? *Animal Cognition*, *18*(1), 291–298. doi: 10.1007/s10071-014-0799-z

Vitousek, M. N., Romero, L. M., Tarlow, E., Cyr, N. E., & Wikelski, M. (2010). Island tameness: An altered cardiovascular stress response in Galápagos marine iguanas. *Physiology & Behavior*, *99*(4), 544–548. doi: 10.1016/j.physbeh.2010.01.016

Walker, B. G., Dee Boersma, P., & Wingfield, J. C. (2006). Habituation of adult Magellanic penguins to human visitation as expressed through behavior and corticosterone secretion: Habituation in Magellanic penguin adults. *Conservation Biology*, *20*(1), 146–154. doi: 10.1111/j.1523-1739.2005.00271.x

Webb, N. V., & Blumstein, D. T. (2005). Variation in human disturbance differentially affects predation risk assessment in Western gulls. *The Condor*, *107*(1), 178–181. doi: 10.1093/condor/107.1.178

Wirén, A., Gunnarsson, U., Andersson, L., & Jensen, P. (2009). Domestication-related genetic effects on social behavior in chickens – Effects of genotype at a major growth quantitative trait locus. *Poultry Science*, *88*(6), 1162–1166. doi: 10.3382/ps.2008-00492

Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. *Advances in the Study of Behavior*, *16*, 229–249. doi: 10.1016/S0065-3454(08)60192-8

CHAPTER 5

Do urban-living yellow mongoose, C*ynictis penicillata,* experience a paradox of choice?



ABSTRACT

The human psycho-economic phenomenon "paradox of choice" suggests that, although having some choice is better than no choice, an abundance of choice is not inevitably more beneficial than a smaller amount of choice. This is because too much choice may result in decision paralysis or dissatisfaction. But, beyond humans, this paradigm has only been extended to non-human primates thus far. The effects of increased choice on animals, especially in an urban context where choice and availability of resources may be greater, remains unknown. I assessed whether urban-dwelling yellow mongooses, *Cynictis penicillata*, experienced a paradox of choice when presented with many food choices. Using cafeteria-style feeding experiments, I investigated their decision-making when presented with various food items offering fewer or more choices. I presented them with 0, 1, 2, or 3 choices and recorded how long it took mongooses to consume the food during each treatment, and their movement patterns among the bowls. The mongooses took longer to make a decision when presented with more choice than they did when presented with only one choice. They also showed evidence of perseveration by repeatedly visiting the same bowls with more choice, and their transitions between the bowls were more structured and predictable with more choice. Overall, mongooses displayed an increased decision-making duration and decision paralysis with too much choice, suggesting that urban mongooses may experience some degree of a paradox of choice and be cognitively challenged when facing an abundance of choice. These results were especially apparent in mongooses occurring in a location with reduced human contact, suggesting different decision-making in areas with lesser and greater human presence.

Keywords: *anthropogenic; choice; decision-making; yellow mongoose*

INTRODUCTION

Cognition entails perception, learning, memory, and decision-making (Shettleworth, 1998). Moment-to-moment decisions, such as which food item to consume, depend on the motivation (both intrinsic and extrinsic) of the individual. Motivation, the internal cues determining which external cues an animal is likely to respond to, will result in an individual being inclined towards one specific activity or item over another (Mason and Bateson, 2009). On the other hand, preference refers to the tendency towards one option, which is usually more desirable, over another (Amdam and Hovland, 2011). This is determined after an assessment of the relative values of available items, when all items have the capability of

satisfying the same motivation (Amdam and Hovland, 2011). Therefore, an animal's motivation to display a particular behaviour, coupled with the preference for a specific option, ultimately results in choice behaviour. In an environment where resources are limited, these decisions may be easy to make – if an animal is hungry and food becomes available, the animal should choose to consume the food. If, however, the number of available options increases, the choice may become slightly more complex. In this case, the choice may depend on the value of the item relative to the alternatives (for example, the energetic value as proposed by the optimal foraging theory; Sih and Christensen, 2001), or on the desirability of the item. Thus, an animal may be better off when more choices become available, since some choice is better than none. This follows the "official dogma" in human psychology and economic theory, which suggests that to maximise one's welfare, one's freedom to choose needs to be maximised (Schwartz, 2007). Moreover, to maximise one's freedom to choose, one's choice needs to be maximised (Schwartz, 2007). However, Schwartz (2007) argues that this "official dogma" is a fallacy.

In what he calls the "paradox of choice", Schwartz (2007) explains that *some* choice is indeed better than *no* choice, but even *more* choice is not necessarily better than *some* choice. Having to choose between many options, one of two situations may arise. Firstly, one may experience paralysis, since too many choices can make it challenging to make decisions. A classic example of such "decision paralysis" is Aesop's fable "The Fox and the Cat". In this fable, the fox is boastful about the magnitude of escape plans he has should he ever need them, while the cat admits that he only knows of one way to escape. When chased down by a pack of hounds, the cat utilises its only escape plan and runs up a tree, successfully evading the hounds. But the fox, scrambling to choose the most efficient escape plan, ends up remaining in place and is soon caught by the hounds and killed by the huntsmen. In this fable, the fox was faced with so many choices that it became paralysed metaphorically and, in the end, chose none. Although his numerous choices seemed beneficial in theory (official dogma), they soon proved disadvantageous (paradox of choice). Secondly, one might be less satisfied with the result of the choice than if there had been less choice (Schwartz et al., 2002; Schwartz, 2007). This may be because choosing one option simultaneously involves rejecting the alternatives (Botti and Iyengar, 2006), the cost of which will increase with the number of available options.

To test these two effects in humans, Iyengar and Lepper (2000) conducted three studies. Firstly, they displayed a limited (6) or extensive (24) number of jam varieties to shoppers. Significantly more customers stopped at the extensive display than the limited

display, yet those that visited the limited display were significantly more likely to purchase one of the jams. Thus, customers were initially more motivated by an extensive display of choices, but ultimately the vast choice was demotivating. Secondly, students were provided with a limited (6) or extensive (30) list of topics from which to write an essay. Significantly more students completed the assignment, and wrote better essays, when they had a limited selection of topics compared with those with the extensive list. Thus, limited-choice students had increased intrinsic motivation when completing the assignment compared with the extensive-choice students, and benefitted more from the limited choice. Finally, they asked participants to choose one chocolate out of a limited (6) or extensive (30) selection of chocolates. Participants took significantly longer to decide when they were given the extensive selection compared with the limited selection. Those participating in the extensive-choice treatment found the experiment more enjoyable, yet frustrating, than those in the limited-choice treatment. Further, they reported significantly reduced satisfaction than the limited-choice participants, but they were still more satisfied than no-choice participants, reiterating the previous statement by Schwartz (2007) that some choice is indeed better than no choice but that even more choice is not necessarily better than some choice. Additionally, participants in the extensive-choice treatment were significantly less likely to accept chocolate over money as compensation for their participation, indicating that extensive choices can lead to individuals opting to choose none. Combined, these results showed that humans are initially attracted to more choice, but they do not benefit from the increased choice, take longer to make decisions, are less satisfied with their decisions, and sometimes avoid choosing at all (decision paralysis).

Yet, humans still prefer more choice over some choice, and more recently, it has been shown that animals have a similar perception of, and preference for, choice (Washburn et al., 1991; Suzuki, 1999; Addessi et al., 2010), even if it is not necessarily beneficial (Perdue and Brown, 2018). For example, capuchin monkeys, *Cebus paella*, and rhesus macaques, *Macaca mulatta*, show a preference for choosing the order in which to complete computerised tasks, rather than having the choice made for them, even when the reward remains the same (Perdue et al., 2014). Thus far, this paradigm has only been extended to non-human primates (Perdue and Brown, 2018), and knowledge of the effects of increased choice on other animals remains largely unknown (Hutchinson, 2005). This is especially important since human welfare is thought to be negatively impacted by extensive choice (Botti and Iyengar, 2006), while such considerations in non-human animals are lacking. Some evidence suggests that increased available choice in calling male painted reed frogs, *Hyperolius marmoratus*, has negative

consequences on female mate selection (Bishop et al., 1995; Hutchinson, 2005), and that larger leks are not as beneficial in increasing the probability of choosing the most popular male as has been previously thought in black grouse, *Tetrao tetrix* (Hutchinson, 2005). Similar studies on foraging decisions are lacking, however.

Experiencing a paradox of choice can occur through various cognitive mechanisms. First, as the number of food choices increases, the relative differences in value (energetic or otherwise) likely decrease as a consequence of probability (Fasolo et al., 2009). For example, if an animal is exposed to 2 different food types, it may prefer one of the two food types (or one food type may be of better quality) and have a simpler choice. However, if an animal is exposed to four food types, the probability of an animal preferring more than one food type over the rest (or the quality of the food types not differing as significantly) increases, thus making the choice more challenging. Secondly, with many available options comes a greater level of comparison, which can be time-consuming and energetically demanding, increasing the potential cost of not choosing correctly (Schwartz, 2007). Third, the second-best option in an extensive-choice scenario may be much more appealing than the second-best option in a limited-choice scenario, again making the choice among the options more challenging (Scheibehenne et al., 2010). These scenarios can lead to decreased motivation to choose, resulting in a paradox of choice.

Generally, decision-making in non-human animals is studied under simple, static conditions that do not adequately reflect an animal's ever-changing natural habitat (Fawcett et al., 2014). These changes might be further exaggerated in urban environments, since food and other resources are abundant (Shochat et al., 2010). As a result, animals are exposed to countless options daily and must make the appropriate decisions to gain maximum benefit. But, do these animals truly benefit from increased choice? Or do they have to engage in more complex cognitive processes to make decisions in urban areas than they would if there were fewer choices? In other words, do they experience a paradox of choice?

To explore these questions, I studied an urban population of yellow mongooses, *Cynictis penicillata*. The yellow mongoose is a small carnivorous mammal (Do Linh San et al., 2015). Its diet consists mainly of small animals such as insects, rodents, reptiles, birds, and amphibians, although it also consumes eggs and carrion (Cavallini and Nel, 1995; Cronk and Pillay, 2018, 2019a, 2019b). In urban habitats, anthropogenic food items, such as bread and dog food, are also consumed (Cronk and Pillay, 2018, 2019a, 2019b). The successful establishment of this species in an urban habitat allowed me to assess decision-making when

presented with various levels of choice through the use of cafeteria-style feeding experiments.

The aim of this experiment was to assess whether urban-dwelling yellow mongooses are cognitively challenged when presented with many food choices. I presented mongooses with cafeteria-style food choice experiments with four levels of choice. This design allowed me to assess whether yellow mongooses experienced the paradox of choice with increased food availability and how this might affect their decision-making. I assessed whether yellow mongooses were cognitively challenged with more choices, and predicted that they would (i) take a longer time to make decisions, (ii) perseverate (i.e. repeat behaviours and behavioural patterns), and (iii) move less predictably and more sporadically between bowls with more choice as their decision-making abilities would be impaired. Additionally, I assessed whether the location of the mongoose colonies affected their decision-making with increased choice and predicted that mongooses in an area of greater human disturbance would (i) have shorter decision latencies, (ii) less perseveration, and (iii) more predictable transitions between bowls with the most choice compared with those in the area of less human disturbance as a result of adaptation to increased resource abundance in their environment.

MATERIALS AND METHODS

Study area

This study took place at two locations in the Meyersdal Nature Area, south of Johannesburg. The Meyersdal Nature Estate (26°18’08.2”S 28°04’55.9”E) consisted of a residential area and a separate, fenced-off nature area in which several yellow mongoose colonies occurred. The Meyersdal Eco Estate (26°17’03.6”S 28°04’50.8”E), separated from the Nature Estate by a double-laned tar road, consisted of residential areas interspersed by nature areas in which mongoose colonies occurred. As a result, mongooses in the Nature Estate were separated from human residents with less human-wildlife contact than those in the Eco Estate, where mongooses encountered humans and other anthropogenic disturbances regularly. A total of 11 sites were selected for this study, six in the Nature Estate and five in the Eco Estate.

Experimental design and protocol

This study took place between June and November 2020 in the Eco Estate, and again February 2023 in the Nature Estate. The experiments were conducted in the mornings between 06h00 and 12h00 since this was when mongooses were the most active (Cronk and Pillay, 2019a, 2020). I used cafeteria-style feeding experiments following a similar methodology to Cronk and Pillay (2018). Meat, egg, dog kibble, and mealworms were selected as the food types for this experiment based on the food choice findings of Cronk and Pillay (2018) in both Meyersdal estates. Equal quantities of food were measured by volume using a teaspoon and placed in four white plastic bowls (12 cm in diameter). The bowls were nailed into the ground 30 cm apart (approximately the average length of the mongoose; Kingdon et al., 2013). Nailing the bowls to the ground prevented them from being moved by the animals or the wind while allowing mongooses to physically move from one bowl to the next, making their decisions more distinct. The bowls were placed in a square configuration (Figure 1) to limit the distance between bowls (both adjacent and diagonal) so that the distance between bowls did not bias mongooses' decision-making when moving from one bowl to the next (i.e. nearest-bowl effect).



Figure 1. Cafeteria-style feeding experimental set-up with four white bowls that contained various or the same food items, presenting mongooses with a choice of food types.

Four treatments were run to provide mongooses with various choices: (i) each bowl containing a different food type (the most choice); (ii) three different food types (intermediate choice; two bowls containing the same food type and the remaining two bowls a different food type each); (iii) two different food types (limited choice; two or three bowls containing the same food type and the remaining two or one bowl(s) a different food type); and (iv) all

four bowls containing the same food type (only one choice). Thus, each treatment provided the mongooses with less choice than the preceding treatment did. After every trial, the food bowls were emptied (if any food remained), cleaned with water if necessary, and replenished with fresh food. The food items used, the order of the food items, and the order of the treatments were randomised for every trial. The bowls were only replaced by new bowls if they were destroyed by mongooses or other animals. A maximum of two trials were conducted per day to prevent satiety leading to decreased motivation to feed. Each treatment was conducted twice at each site, and the experiment was run concurrently at all sites per location.

Browning® Trail Cameras (Model BTC-8A; 55° field of view; Browning, 2019) triggered with a motion sensor were set up between 1 and 2 m away from the experiment, ensuring that the entire feeding station was in view of the camera. Each trial started as soon as a mongoose entered the camera's field of view (1 – 2 m across) and ended as soon as the mongoose exited the camera's view after consuming all the food. From the video footage, the following was recorded: (i) the latency to investigate the first food bowl, recorded as the number of seconds that elapsed since the mongoose first entered the camera's frame to when it first interacted with a food bowl (had its snout over the bowl); (ii) the latency to consume the first food, recorded as the number of seconds elapsed from when the mongoose first interacted with a food bowl to when it started feeding on the first food item; (iii) the first bowl investigated by the mongoose followed by the sequence in which bowls were investigated; and (iv) the bowl from which the mongoose fed first followed by the sequence in which the bowls were fed from. The straight-line distance between each site and the nearest human residence was measured using Google Earth™ and was used to detect a proximity to human residential effect.

Data analyses

All statistical analyses were conducted using R Statistical Software (R version 3.4.3; R Core Team, 2013; http://www.R-project.org/). Shapiro-Wilk tests were used to test for normality. Non-normal variables were transformed using a Box-Cox transformation (R package: MASS), and if variables could not be transformed, non-parametric tests were used. Generalised linear mixed models (GLMMs) were used to analyse differences in the (i) latency to investigate and (ii) latency to consume the first food between the four treatments in each location (family = Gaussian; link = identity). The various treatments were a repeated

measures design, with treatment and location as fixed effects, site and trial as random effects, and proximity as a covariate. General linear hypothesis testing (glht) and Tukey post hoc tests were used to determine pairwise differences for significant fixed factors (R package: multcomp).

Perseveration (i.e. repeated visitations to the same bowl) was analysed using spontaneous alternation behaviour (SAB) scores. This was only done for the patterns of investigating the bowls (not for the patterns of consuming the food) since perseveration behaviour would be expected during the initial decision-making process. SAB scores were calculated as the ratio of actual bowls being visited to the possible number of bowls that could have been visited in a sequence, following the method used by Jones et al. (2011). Thus, if the bowl visitation sequence was *abcdc…abc*, the SAB scores were calculated as follows: during the first tetrad (***abcd****c…abc*), the mongoose visited 4 bowls of a possible 4, and thus the SAB score would be 4/4 = 1; for the second tetrad (*a****bcdc****…abc*), the mongoose only visited 3 bowls of a possible 4, thus receiving an SAB score of 3/4 = 0.75, and so on; the final three bowl visitations in this sequence would not be considered since it did not make up a complete tetrad. The average SAB scores were then calculated for each treatment in each location. A low SAB score suggested that a limited number of bowls were visited and that the same bowl was visited repeatedly more often, indicative of perseveration, whereas a high SAB score suggested that more bowls were visited evenly. GLMMs were used to analyse whether SAB scores differed among the treatments in each location (family = Gaussian; link = identity), with treatment and location as fixed effects, and site and trial as random effects. General linear hypothesis testing (glht) and Tukey post hoc tests were used to determine pairwise differences for significant fixed factors.

Sixteen sequential transition matrices were generated (using Matman^{TM}; Noldus Information Technology), each capturing the sequence of either investigating the bowls or consuming the food for each treatment (summed over sites and trials) and in each location. These transitions were generated to visualise the moment-to-moment decisions as mongooses moved from one bowl to the next during each treatment. After the normalisation of the matrices, the adjusted residuals between the observed and expected values for each transition frequency in each of the sixteen matrices were calculated and expressed as a z-distribution. Positive residuals suggested that the transitions occurred more often than by chance, whereas negative residuals suggested that the transitions occurred less often than by chance. From these results, graphical representations of the positive transitions when investigating the bowls and consuming the food were produced for each treatment and location.

Ethical approval

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2019/05/35/B).

RESULTS

The yellow mongooses (n = 11) in this study engaged with the experiment in both estates during most trials. However, trials during which the food was not consumed, or only some bowls were visited, were excluded from the analyses (i.e. only trials that were completed successfully were analysed and included in this study). Furthermore, in trials where the mongooses did not visit the experiment for an extended period, the food was often consumed by ants before the mongooses returned, or the mongooses were disturbed by ants when attempting to feed from the food bowls, resulting in these trials also being excluded from any analyses. During most trials, only one mongoose visited the experiment, but sometimes two or three mongooses visited the bowls. Trials with multiple mongooses were analysed for one mongoose only - the focal individual was easily identified as the individual consuming food from all four bowls, typically exhibiting aggression towards and driving away the other individual(s). Mongooses did not display any neophobia towards the food bowls, likely owing to previous food preference and pilot experiments conducted using identical bowls.

Latency to investigate

The latency to investigate the first food bowl was measured as the number of seconds that elapsed from the moment a mongoose entered the camera's field of view until it first contacted a food bowl. This was indicative of the decision-making response time. Location ($\chi^2 = 4.00$, df = 1, p = 0.046; Figure 2a), treatment ($\chi^2 = 10.77$, df = 3, p = 0.013; Figure 2b), and the interaction between location and treatment ($\chi^2 = 21.81$, df = 3, $p < 0.001$; Figure 3) were significant predictors of the latency to investigate the first bowl, whereas the proximity to the nearest human residents was not ($\chi^2 = 1.49$, df = 1, p = 0.222). The latency to investigate the first food bowl was significantly longer in the Nature Estate compared with the Eco Estate (Figure 2a). Additionally, the latency to investigate the first food bowl was significantly longer when there were two (z = -2.85, p = 0.023) or four (z = -2.71, p = 0.035) different food types compared with only one food type (Figure 2b).

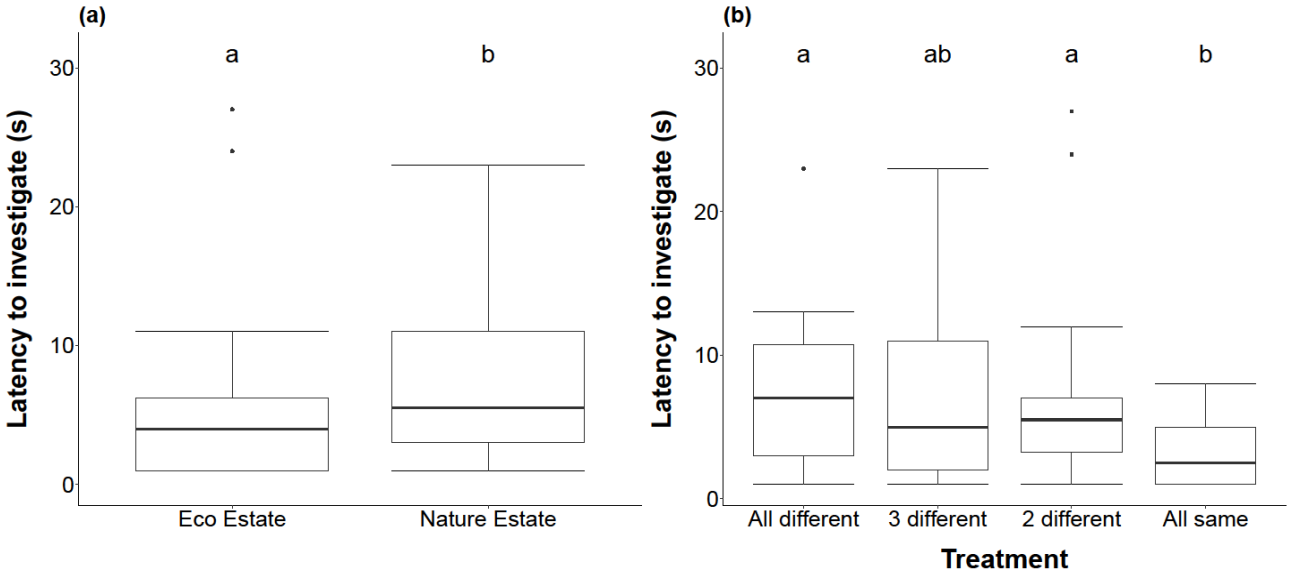


Figure 2. The latency to investigate the first bowl by yellow mongooses during a paradox of choice experiment in **(a)** the Meyersdal Eco Estate and Meyersdal Nature Estate during **(b)** four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.

The latency to investigate the first bowl was significantly longer in the Nature Estate compared with the Eco Estate when there were three different food types ($t = -3.48$, $p = 0.044$; Figure 3). In the Nature Estate, the latency to investigate the first bowl was significantly longer when there were four ($t = 3.60$, $p = 0.014$) or three ($t = 4.11$, $p = 0.003$) food types compared with only one food type.

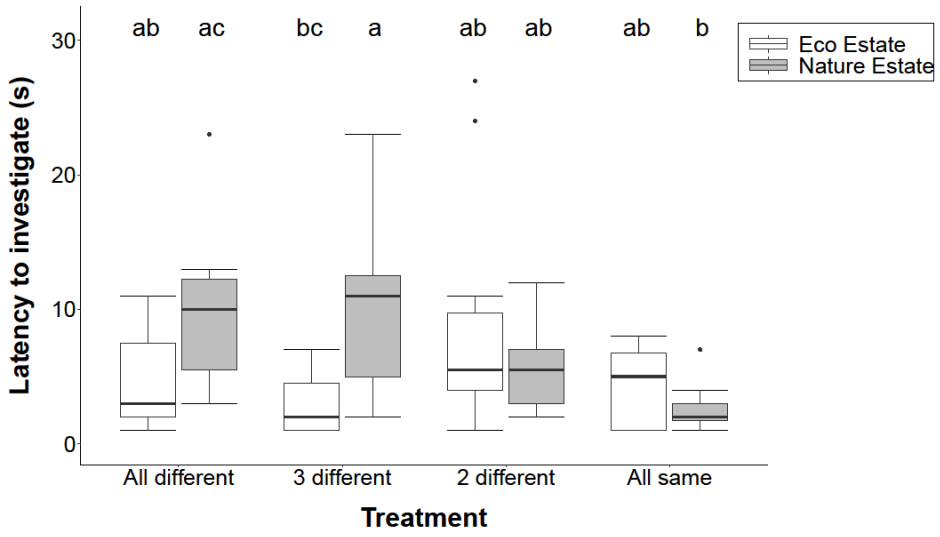


Figure 3. The latency to investigate the first bowl by yellow mongooses during a paradox of choice experiment in the Meyersdal Eco Estate (white boxes) and Meyersdal Nature Estate (grey boxes) during four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.

Latency to consume

The latency to consume the first food item was measured as the number of seconds that elapsed from the moment a mongoose investigated the bowls until it first consumed a food item. Location (χ^2 = 7.98, df = 1, p = 0.005; Figure 4a), treatment (χ^2 = 31.49, df = 3, p < 0.001; Figure 4b), and the interaction between location and treatment (χ^2 = 37.92, df = 3, p < 0.001; Figure 5) were significant predictors of the latency to consume the first food, whereas the proximity to the nearest human residents was not (χ^2 = 0.16, df = 1, p = 0.745). The latency to consume the first food was significantly longer in the Nature Estate compared with the Eco Estate (Figure 4a). Additionally, the latency to consume the first food was significantly longer when there were four (z = -2.85, p = 0.022) or three (z = -4.95, p < 0.001) different food types compared with only one food type, and when there were three different food types compared with two food types (z = -4.48, p < 0.001; Figure 4b).

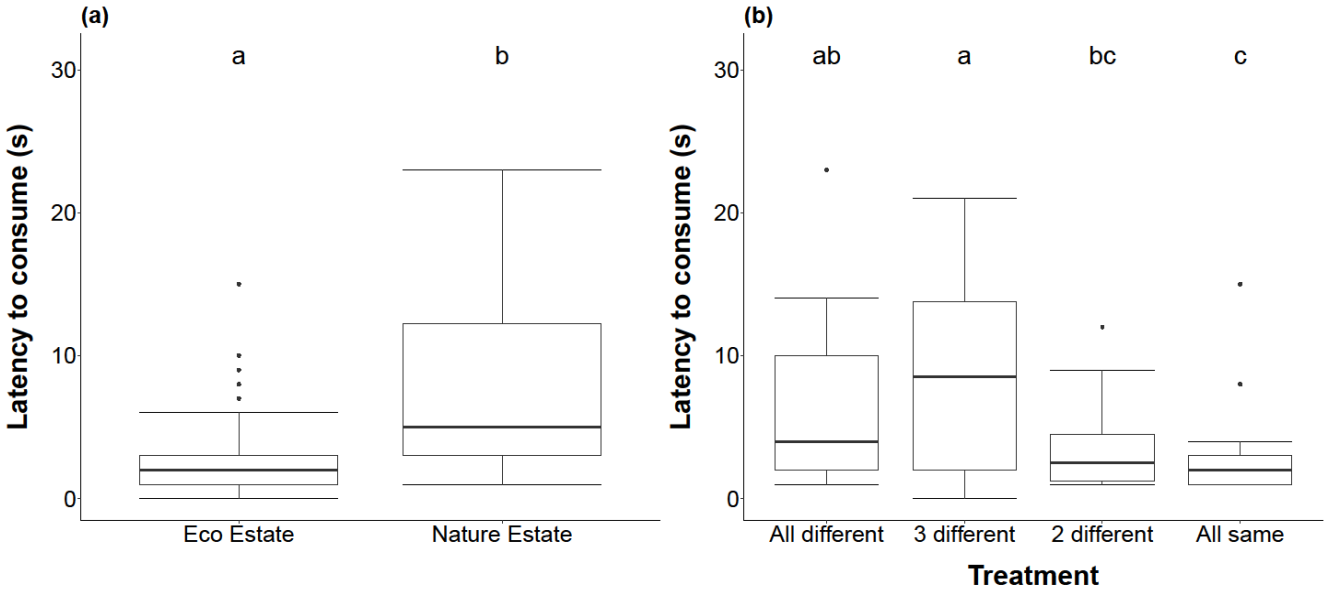


Figure 4. The latency to consume food from the first bowl by yellow mongooses during a paradox of choice experiment in **(a)** the Meyersdal Eco Estate and Meyersdal Nature Estate during **(b)** four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.

The latency to consume the first food when there were three food types was significantly longer in the Nature Estate compared with all other treatments in the Eco Estate (four food types: $t = -5.01$, $p = 0.002$; three food types: $t = -4.84$, $p = 0.003$; two food types: $t = 4.93$, $p = 0.002$; one food type: $t = 4.54$, $p = 0.005$; Figure 5) as well as when there were two ($t = 6.17$, $p < 0.001$) or only one food type ($t = 7.40$, $p < 0.001$) in the Nature Estate. Furthermore, the latency to consume the first food was significantly longer when there were four food types compared with two ($t = 3.49$, $p = 0.020$) or only one food type ($t = 4.72$, $p < 0.001$) in the Nature Estate.

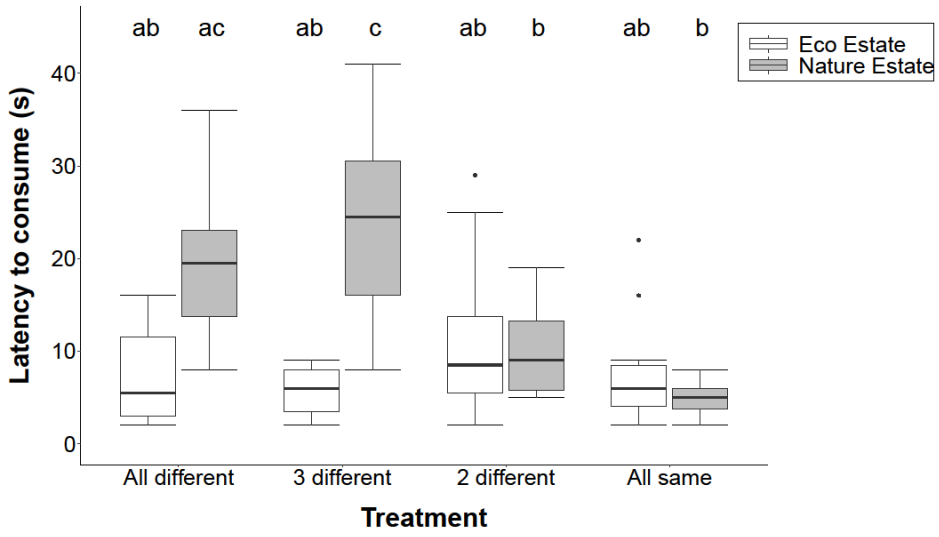


Figure 5. The latency to consume the first food by yellow mongooses during a paradox of choice experiment in the Meyersdal Eco Estate (white boxes) and Meyersdal Nature Estate (grey boxes) during four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.

Spontaneous Alternation Behaviour (SAB) Scores

The spontaneous alternation behaviour (SAB) score indicated whether mongooses visited the same bowl repeatedly. Location (χ^2 = 5.92, df = 1, p = 0.015; Figure 6a), treatment (χ^2 = 11.87, df = 3, p = 0.007; Figure 6b), and the interaction between location and treatment (χ^2 = 8.60, df = 3, p = 0.035; Figure 7) were significant predictors of the latency to consume the first food. The SAB score was significantly lower in the Nature Estate compared with the Eco Estate (Figure 6a). The SAB score was significantly lower when there were four food types compared with two (z = 2.82, p = 0.025) or only one food type (z = 2.66, p = 0.039; Figure 6b).

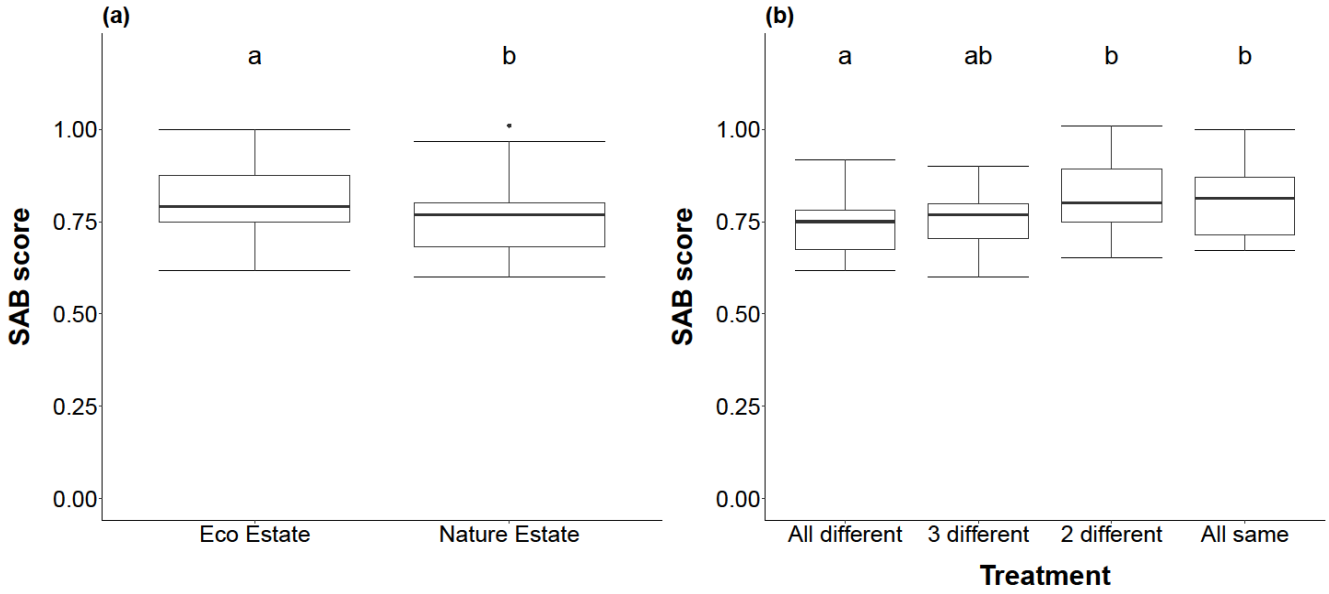


Figure 6. SAB scores for the sequence in which the bowls were investigated by yellow mongooses during a paradox of choice experiment in **(a)** the Meyersdal Eco Estate and Meyersdal Nature Estate during **(b)** four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.

The SAB score was significantly lower when there were four food types compared with two food types in the Nature Estate ($t = -3.18$, $p = 0.045$) or only one food type in the Eco Estate ($t = -3.86$, $p = 0.019$; Figure 7). Furthermore, the SAB score was significantly lower when there were three food types in the Nature Estate compared with only one food type in the Eco Estate ($t = -3.53$, $p = 0.037$).

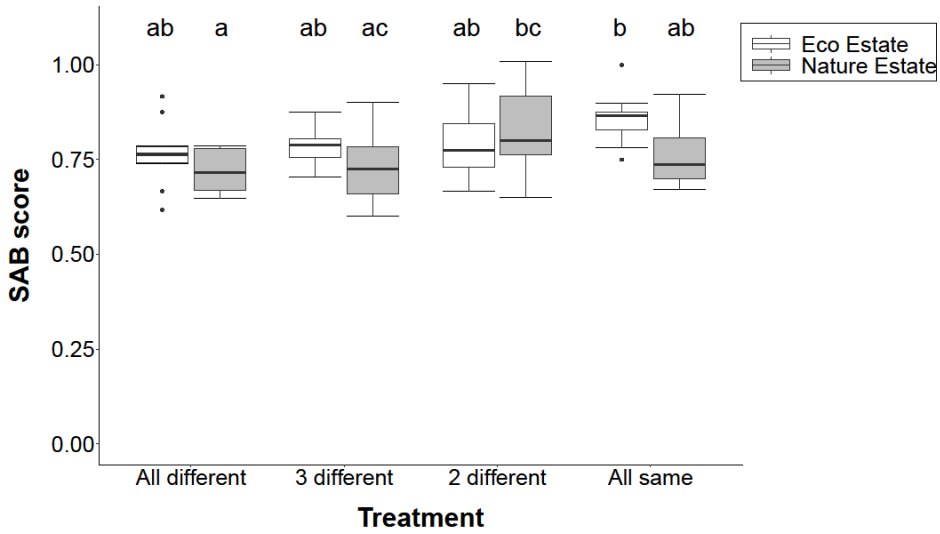


Figure 7. SAB scores for the sequence in which the bowls were investigated by yellow mongooses during a paradox of choice experiment in the Meyersdal Eco Estate (white boxes) and Meyersdal Nature Estate (grey boxes) during four different treatments. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, and the error bars indicate confidence intervals. The same alphabet letters indicate no significant difference between locations or treatments.

Transition matrices

Order of investigating

Transition matrices indicated whether the transitioning from one bowl to another was significantly more likely than predicted by chance. In the Eco Estate, the mongooses were most likely to move between the adjacent bowls A and B, and from bowl D to the adjacent bowl C during the most choice (all different; Figure 8). With three choices, the mongooses were most likely to move from bowl C to the adjacent bowl A, and from bowl B to the adjacent bowl D. When mongooses had two choices, they were most likely to move from bowl A to the adjacent bowl C, and from bowl B to the adjacent bowl D. With only one choice (all same), mongooses were most likely to move from bowl A to the adjacent bowl B, and from bowl C to the adjacent bowl D. In the Nature Estate, the mongooses were most likely to move from bowl A to the adjacent bowl B, and from bowl D to the adjacent bowl C during the most choice (all different; Figure 8). With three choices, mongooses were most likely to move from bowl A to the adjacent bowl B, and from bowl B to the adjacent bowl D. When mongooses had two choices, they were most likely to move from bowl A to the adjacent bowl C. With only one choice (all same), mongooses were most likely to move from

bowl A to the adjacent bowl B, and from bowl B to the adjacent bowl D. These transition sequences occurred independent of the food choice since the food types were randomised in the bowls, and there were no significant diagonal transitions.

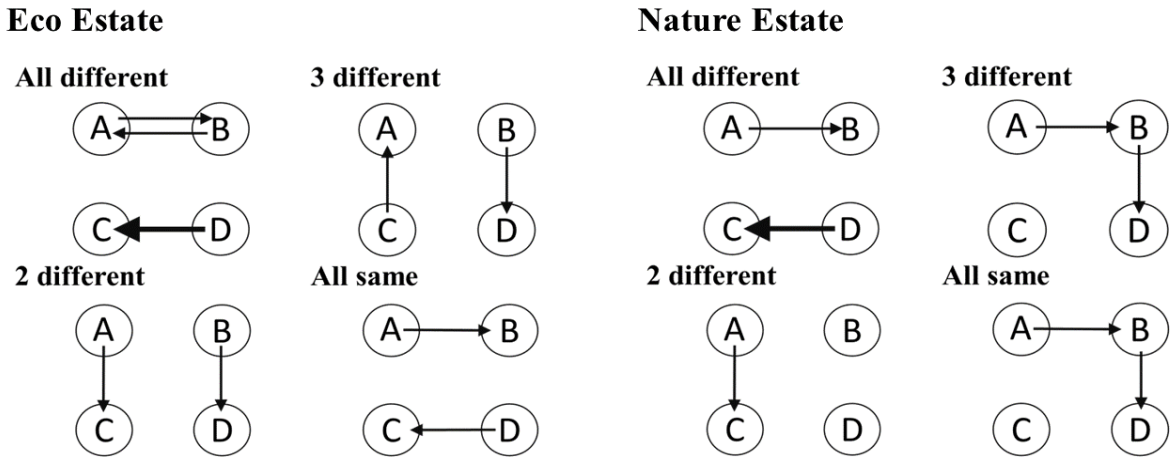


Figure 8. Transitions when food bowls were investigated by yellow mongooses in the Meyersdal Eco Estate and the Meyersdal Nature Estate during a paradox of choice experiment. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The circles indicate bowls, and the letters A – D indicate the sequence of the four bowls (not the food types, which were randomised in the bowls). Arrows indicate a significant transition to move from one bowl to the next in the direction of the arrow. The thickness of the lines is representative of the level of significance, with thin lines being significant ($p < 0.05$) and thicker lines being highly significant ($p < 0.01$).

Order of consuming

The order in which mongooses consumed the food items indicated their final decision when presented with various food items. In the Eco Estate, the mongooses were most likely to move between the adjacent bowls A and B, and from bowl D to the adjacent bowl C with the most choice (all different; Figure 9). With three choices, mongooses were most likely to move from bowl C to the adjacent bowl A, and from bowl B to the adjacent bowl D. When mongooses had two choices, they were most likely to move from bowl A to the adjacent bowl C, and from bowl B to the adjacent bowl D. With only one choice (all same), mongooses were most likely to move from bowl A to the adjacent bowl B, bowl B to the adjacent bowl D, bowl D to the adjacent bowl C, and bowl C to the adjacent bowl A. In the Nature Estate, mongooses were most likely to move from bowl A to the adjacent bowl B, and from bowl D to the adjacent bowl C during the most choice (all different; Figure 9). With three choices,

mongooses were most likely to move from bowl A to the adjacent bowl C, and from bowl B to the adjacent bowl D. When mongooses had two choices, they were most likely to move from bowl A to the adjacent bowl C, and from bowl B to the adjacent bowl D. With only one choice (all same), mongooses were most likely to move from bowl A to the adjacent bowl B, from bowl B to the adjacent bowl D or diagonally to bowl C, and from bowl D to the adjacent bowl C. Again, these transition sequences occurred independent of the food choice since the food types were randomised in the bowls. The majority of the transitions occurred between adjacent bowls with only one significant diagonal transition with only one choice in the Nature Estate.

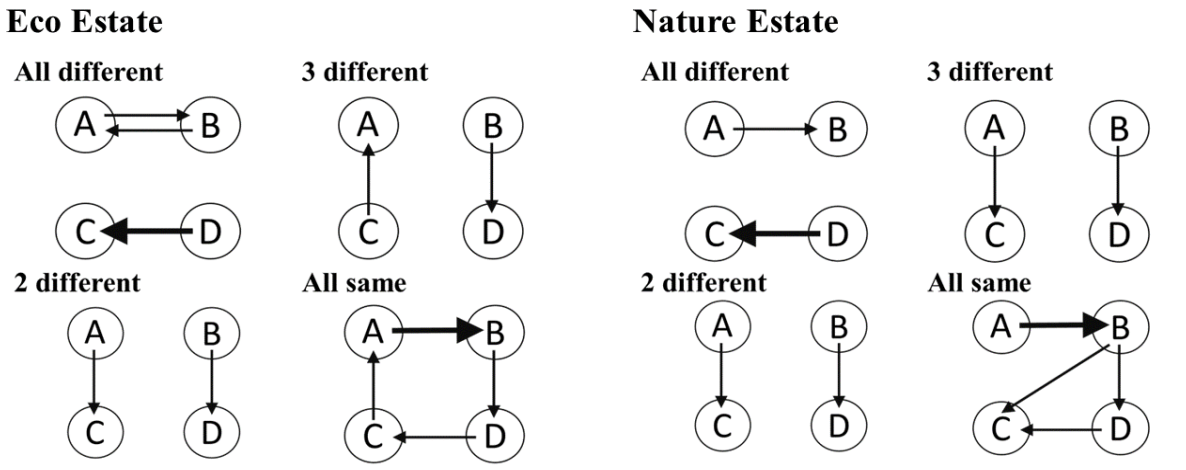


Figure 9. Transitions when food was consumed from four bowls by yellow mongooses in the Meyersdal Eco Estate and the Meyersdal Nature Estate during a paradox of choice experiment. The treatments included (i) treatment 1: all four bowls containing a different food item; (ii) treatment 2: three different food types among the four bowls; (iii) treatment 3: two different food types among the four bowls; (iv) treatment 4: all four bowls containing the same food type. The circles indicate bowls, and the letters A – D indicate the sequence of the four bowls (not the food types, which were randomised in the bowls). Arrows indicate a significant transition to move from one bowl to the next in the direction of the arrow. The thickness of the lines is representative of the level of significance, with thin lines being significant ($p < 0.05$) and thicker lines being highly significant ($p < 0.01$).

DISCUSSION

I investigated yellow mongooses' decision-making when presented with many food choices to establish whether they experience the human psycho-economic phenomenon known as the paradox of choice by displaying some level of impairment in their decision-making abilities. The mongooses in the Nature Estate took longer to make a decision than those in the Eco

Estate, particularly during increased choice. Furthermore, mongooses took the longest to make a decision when they had the most choice (four choices) or limited choice (two choices), and were the quickest at making a decision with only one choice. After the initial decision-making, mongooses in the Nature Estate took longer to consume the food than those in the Eco Estate. The mongooses were the quickest to consume the food when they only had one choice and took the longest with more choice (three and four food types). The spontaneous alternation behaviour (SAB) scores revealed that mongooses in the Nature Estate made more repeat visits to the same bowl, particularly when they had more choice, than those in the Eco Estate who did not perseverate. Lastly, transitions between bowls indicated more significant positive and bidirectional transitions with more choice, possibly indicating more predictable decisions with more choice.

When deciding on which food item to consume, two distinct central decision-points exist: firstly, which bowl to investigate first, and secondly, which food to consume first. The mongooses' choice was revealed by the first decision-point, whereas the second decision-point provided information about the mongooses' response towards their choice. I expected the first decision-point, measured as the latency to investigate, to take longer when presented with the most choice since mongooses are likely to experience difficulty with making a decision if they experience a paradox of choice. As predicted, the mongooses took the longest to make a decision when they were presented with the most choice (four different food types) and two choices, and were the quickest when they had only one choice (four of the same food). My results are consistent with the results from Iyengar and Lepper (2000), who found that humans take longer to make a decision when given an extensive selection of chocolates.

Iyengar and Lepper (2000) proposed two potential strategies for the decision-making process during limited- and extensive-choice scenarios in humans, which could also apply to non-human animals. Individuals can either use an optimising strategy, whereby limited-choice decisions involve choosing the most ideal or optimal choice, or a satisficing strategy, whereby extensive-choice decisions involve choosing any acceptable option that will satisfy the relevant motivation to avoid cognitive overload. If this were the case in animals, I would expect individuals to take longer to make a decision when exposed to some choice, but to make decisions quicker with an overwhelming amount of choice. However, it appears that the mongooses in the Nature Estate were weighing up their options before choosing a particular food, specifically when multiple options were available (likely using an optimising strategy), whereas those in the Eco Estate took no longer to choose a particular food type than when they had only one choice (likely using a satisficing strategy).

Decision paralysis, the inability to choose between options, is the consequence of a decline in the motivation to choose, with motivation decreasing as the number of available options increases (Iyengar and Lepper, 2000). Consequently, animals with initially higher motivation to feed (e.g. malnourished, scarcity of resources; McNamara et al., 2012) may still be more motivated to choose an option than those who are initially less motivated even when experiencing decision paralysis. With more available choices, I expected mongooses to spend more time making a decision. However, mongooses in the Eco Estate took no longer to choose when they had the most choice than when they had only one choice, suggesting that they chose the first available option without first weighing up their options. This absence of active decision-making with any number of available choices may reflect reduced motivation to choose in mongooses in the Eco Estate (which may have been more well-fed), even at lower levels of choice, compared with those in the Nature Estate. This may be the result of a satisficing decision-making strategy which is consistent with the definition of "decision paralysis" whereby animals avoid making a decision at all, but may be adaptive in urban-living mongooses that are exposed to increased resource availability.

The second decision-point, measured as the latency to consume, differed significantly with the number of choices in the Nature Estate, following a similar pattern to their initial decision latencies, but not in the Eco Estate. Thus, when mongooses were quick to make a decision, they were also quick to act on that decision, but longer decisions required more time before consumption. When deciding which food item to consume in the face of numerous options, an individual must assess the relative value of the options (Sih and Christensen, 2001; Amdam and Hovland, 2011). In doing so, factors such as relative energetic value and preference must be considered (Sih and Christensen, 2001; Amdam and Hovland, 2011). This choice can happen in one of two ways: either the individual consumes the first food it encounters, or it consumes the most preferred food item first. However, spending too much time and energy on making a decision about which food item to consume has its own costs, such as the increased risk of predation resulting in the animal having to abandon the food, or having the food taken away by a conspecific (Stephens, 2002). After the initial decision was made, it appeared that mongooses did not spend additional time contemplating their decision in the Eco Estate, which may be beneficial in minimising the potential effects of a paradox of choice. However, when mongooses in the Nature Estate experienced difficulties during the initial decision-point, they experienced similar difficulties during the second decision-point. This could indicate reduced satisfaction with the outcome of their initial decision with more choices (three and four food types).

SAB scores are indicative of perseveration, which could potentially indicate that mongooses were cognitively challenged, as would be expected when experiencing a paradox of choice. Perseveration refers to the repetition of the same behaviour (Hauser, 1999), even if the particular behaviour is not beneficial in solving the current problem. Animals that exhibit more perseverations are typically less behaviourally flexible, are more likely to show stereotypic behaviours, and have decreased inhibitory control (Jones et al., 2011). Therefore, if an animal lacks the necessary behavioural flexibility or inhibitory control to make appropriate decisions, as a result of high levels of perseveration with the increased choice characteristic of urban environments, the results may be detrimental (e.g. Aesop's fox). I used perseveration as a measure of being cognitively challenged since it is unaffected by motivation (Hauser, 1999). Thus, although individuals are initially more motivated by increased choice (e.g. humans are more attracted to the extensive jam display; Iyengar and Lepper, 2000), or as the result of malnutrition, this motivation would not have affected the perseveration observed in the mongooses in this study. The higher SAB score when mongooses were presented with only one choice suggests more random visitations to the various bowls (with the visitations distributed evenly among the bowls), whereas the lower SAB score when presented with the most choice suggests more repetitive visitations to the same bowl. These repetitive visitations indicate perseveration in mongooses when faced with many choices. Furthermore, mongooses in the Nature Estate were more likely to perseverate than those in the Eco Estate, particularly with the most choice. Interestingly, the mongooses in the Nature Estate exhibited comparable perseveration scores with only one choice as they did with the most choice, and they were the least likely to perseverate with two choices. Since it is unlikely that perseveration was related to differences in motivation to feed, these results may indicate that mongooses in the Eco Estate are adapted to greater food availability while those in the Nature Estate experience difficulties with decision-making when presented with extensive choice.

Transition matrices, which indicate the probability of one transition following another transition between bowls, were used to assess the mongooses' moment-to-moment decisions when moving between the bowls. I expected irregular and sporadic transitions of the mongooses among bowls when presented with the most choice, as mongooses are expected to experience difficulty with decision-making if they experience a paradox of choice. Instead, more predictable and structured movement patterns were observed with the most choice, indicating an absence in decision-making altogether. The mongooses in the Eco Estate had the most significant positive and bidirectional transitions during their initial decision-making

with the most choice. Further, they were most likely to move from one bowl to an adjacent bowl, never crossing over to the bowl diagonally from the current bowl. These patterns suggest a nearest-bowl effect as opposed to a decision effect, where mongooses likely based their movement patterns on the next nearest bowl, as opposed to some alternative decisions such as food preference. Even so, the mongooses only showed a pattern of moving from one bowl to the next continuously (from A to B to C to D and back to A, with no diagonal transitions) when consuming the food with only one choice, a pattern that would be expected in the complete absence of decision-making. In the Nature Estate, mongooses had more significant positive transitions in most choice tests, and their transitions were the least predictable when they had a choice of two food types. It is possible that these mongooses were best able to choose, and thus direct their behaviour more intentionally, when they only had to weigh up two options, which is further supported by the large SAB score with two food types. Additionally, the active decision-making diminished with only one choice, resulting in mongooses transitioning from one bowl to the next nearest bowl. The mongooses' moment-to-moment decisions, through the greater frequency of transitions and occurrence of bidirectional transitions with the most choice and only one choice, support more predictable patterns of movement between the bowls, possibly indicating decision paralysis (i.e. reducing their active decision-making and simply moving in a predictable fashion between the bowls) in both locations.

There is some scepticism as to whether the paradox of choice exists in humans after a meta-analysis of 50 studies considering "choice overload" by Scheibehenne et al. (2010), let alone the existence of this phenomenon in non-human animals. However, Scheibehenne et al. (2010) pointed out several discrepancies in the studies reviewed, and suggested a number of factors that could influence human decision-making during such experiments, for example the experimental set-up, the decision-making methods used, and the decision-maker's perception. An important factor that is often neglected in these human-based studies is time pressure when choosing, an issue that may be critical in non-human animal decisions. Haynes (2009) showed that choice overload is more likely to occur when human participants are constrained by time when making a decision. Similarly, animals are under time pressure when making foraging decisions, especially in the presence of conspecific competitors or predators (Stephens, 2002). Hutchinson (2005) furthermore suggested that free-living animals are unlikely to experience a paradox of choice since animals are adapted to the level of choice found in their natural environment. However, urban animals face unique challenges and environmental changes, one of which is a greater availability of food, thus increasing the

chances of an animal facing an abundance of choice and potentially encountering a paradox of choice. Yet, this increased choice may be cognitively demanding when having to choose between various food items, especially when such choice was not part of their evolutionary past, negatively affecting their ability to make decisions. Iyengar and Lepper's (2000) jam experiment, for example, was conducted at a grocery store known for its wide variety of products. Still, even though customers knowingly chose a store with a seemingly unlimited choice of products, the increased choice in their experiment negatively affected them.

Similar to the experiments by Iyengar and Lepper (2000), non-human animals may initially be more attracted to increased choice, but it may ultimately be detrimental to their intrinsic motivation when having to choose. If animals are cognitively challenged by greater choice to such an extent that making a decision is more costly than waiting for an easier decision, opting not to choose may be an adaptive strategy (Hutchinson, 2005), especially in urban areas where the probability of encountering alternative food options is elevated. In this case, a difficult decision, combined with time pressure increasing the probability of decision paralysis, may be resolved by leaving in search of alternative opportunities to make an easier decision (i.e. abandoning the food altogether). However, the costs associated with investing in presently unavailable options (opportunity costs; Stephens, 2002) may outweigh the benefits of simply consuming the food first encountered and avoiding decision-making altogether. As a result, animals may face cognitive challenges when they encounter an abundance of choices, which may be disadvantageous when making important survival decisions, for instance, which food to consume. However, this limited capacity in decision-making may also benefit animals by allowing them to respond quickly in situations where faster response times may be more beneficial than selecting the optimal choice.

The mongooses in my study showed evidence of a paradox of choice by being cognitively challenged with increased choice, especially those occurring in the Nature Estate, where interaction with humans is reduced. Mongooses took longer to make decisions with increased choices and appeared to perseverate when the choices increased to more than two choices. The transitions were more predictable and structured with more choice, likely due to decision paralysis. The mongooses in my study responded differently to decision-making scenarios in areas with differing levels of human disturbance. This may reflect changes in decision-making in response to increased available choices by using a satisficing strategy or simply decreased motivation to choose. More studies should consider the prevalence of a paradox of choice in free-living, non-human animals, particularly in an urban context when

food abundance is inevitable. Furthermore, whether this phenomenon is adaptive or harmful is uncertain, which could have important implications for animal welfare.

REFERENCES

Addessi, E., Mancini, A., Crescimbene, L., Ariely, D., & Visalberghi, E. (2010). How to spend a token? Trade-offs between food variety and food preference in tufted capuchin monkeys (*Cebus apella*). *Behavioural Processes*, *83*(3), 267–275. doi: 10.1016/j.beproc.2009.12.012

Amdam, G. V., & Hovland, A. L. (2011). Measuring animal preference and choice behaviour. *Nature Education Knowledge*, *3*(10), 74.

Bishop, P. J., Jennions, M. D., & Passmore, N. I. (1995). Chorus size and call intensity: Female choice in the painted reed frog, *Hyperolius Marmoratus*. *Behaviour*, *132*(9–10), 721–731. doi: 10.1163/156853995X00117

Botti, S., & Iyengar, S. S. (2006). The dark side of choice: When choice impairs social welfare. *Journal of Public Policy & Marketing*, *25*(1), 24–38. doi: 10.1509/jppm.25.1.24

Browning. (2019). *Browning Trail Cameras: Advantage SpecOps Full HD Video Model BTC-8A: Instruction Manual*. Browning. Retrieved from https://browningtrailcameras.zendesk.com/hc/en-us/article_attachments/360073084653/Spec_Ops_Advantage_BTC-8A.pdf

Cavallini, P., & Nel, J. A. J. (1995). Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). *South African Journal of Zoology*, *30*(2), 46–49. doi: 10.1080/02541858.1995.11448371

Cronk, N. E., & Pillay, N. (2018). Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethologica*, *21*(2), 127–136. doi: 10.1007/s10211-018-0291-x

Cronk, N. E., & Pillay, N. (2019a). Flexible use of urban resources by the yellow mongoose *Cynictis penicillata*. *Animals*, *9*(7), 447. doi: 10.3390/ani9070447

Cronk, N. E., & Pillay, N. (2020). Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment. *Journal of Urban Ecology*, *6*(1), 1–9. doi: 10.1093/jue/juaa013

Cronk, N., & Pillay, N. (2019b). Dietary overlap of two sympatric African mongoose species in an urban environment. *Mammalia*, *85*(5), 428–438. doi: 10.1515/mammalia-2018-0113

Do Linh San, E., Cavallini, P., & Taylor, P. (2015). *The IUCN Red List of Threatened Species 2015* [Data set]. International Union for Conservation of Nature. doi: 10.2305/IUCN.UK.2015-4.RLTS.T41597A45205726.en

Fasolo, B., Hertwig, R., Huber, M., & Ludwig, M. (2009). Size, entropy, and density: What is the difference that makes the difference between small and large real-world assortments? *Psychology and Marketing*, *26*(3), 254–279. doi: 10.1002/mar.20272

Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C., & McNamara, J. M. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences*, *18*(3), 153–161. doi: 10.1016/j.tics.2013.12.012

Hauser, M. D. (1999). Perseveration, inhibition and the prefrontal cortex: A new look. *Current Opinion in Neurobiology*, *9*(2), 214–222. doi: 10.1016/S0959-4388(99)80030-0

Haynes, G. A. (2009). Testing the boundaries of the choice overload phenomenon: The effect of number of options and time pressure on decision difficulty and satisfaction. *Psychology and Marketing*, *26*(3), 204–212. doi: 10.1002/mar.20269

Hutchinson, J. M. C. (2005). Is more choice always desirable? Evidence and arguments from leks, food selection, and environmental enrichment. *Biological Reviews*, *80*(1), 73–92. doi: 10.1017/S1464793104006554

Iyengar, S. S., & Lepper, M. R. (2000). When choice is demotivating: Can one desire too much of a good thing? *Journal of Personality and Social Psychology*, *79*(6), 995–1006. doi: 10.1037/0022-3514.79.6.995

Jones, M. A., Mason, G. J., & Pillay, N. (2011). Correlates of birth origin effects on the development of stereotypic behaviour in striped mice, *Rhabdomys*. *Animal Behaviour*, *82*(1), 149–159. doi: 10.1016/j.anbehav.2011.04.010

Kingdon, J., Happold, D., Butynski, T., Hoffman, M., Happold, M., & Kalina, J. (Eds.). (2013). *Cynictis penicillata*, Yellow Mongoose. In *Mammals of Africa. Vol. 5: Carnivores, pangolins, equids and rhinoceroses* (pp. 334–339). London: Bloomsbury.

Mason, G., & Bateson, M. (2009). Motivation and the organization of behaviour. In *The Ethology of Domesticated Animals* (2nd ed., pp. 38–56). Wallingford, UK: CAB International.

McNamara, J. M., Trimmer, P. C., & Houston, A. I. (2012). The ecological rationality of state-dependent valuation. *Psychological Review*, *119*(1), 114–119. doi: 10.1037/a0025958

Perdue, B. M., & Brown, E. R. (2018). Irrational choice behavior in human and nonhuman primates. *Animal Cognition*, *21*(2), 227–234. doi: 10.1007/s10071-017-1156-9

R Core Team. (2013). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.R-project.org/

Scheibehenne, B., Greifeneder, R., & Todd, P. M. (2010). Can there ever be too many options? A meta-analytic review of choice overload. *Journal of Consumer Research*, *37*(3), 409–425. doi: 10.1086/651235

Schwartz, B. (2007). *The paradox of choice: Why more is less* (Reissued). New York, NY: Harper Perennial.

Schwartz, B., Ward, A., Monterosso, J., Lyubomirsky, S., White, K., & Lehman, D. R. (2002). Maximizing versus satisficing: Happiness is a matter of choice. *Journal of Personality and Social Psychology*, *83*(5), 1178–1197. doi: 10.1037/0022-3514.83.5.1178

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.

Shimojo, S., Simion, C., Shimojo, E., & Scheier, C. (2003). Gaze bias both reflects and influences preference. *Nature Neuroscience*, *6*(12), 1317–1322. doi: 10.1038/nn1150

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., & Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, *60*(3), 199–208. doi: 10.1525/bio.2010.60.3.6

Sih, A., & Christensen, B. (2001). Optimal diet theory: When does it work, and when and why does it fail? *Animal Behaviour*, *61*(2), 379–390. doi: 10.1006/anbe.2000.1592

Stephens, D. W. (2002). Discrimination, discounting and impulsivity: A role for an informational constraint. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1527–1537. doi: 10.1098/rstb.2002.1062

Suzuki, S. (1999). Selection of forced- and free-choice by monkeys (*Macaca fascicularis*). *Perceptual and Motor Skills*, *88*(1), 242–250. doi: 10.2466/pms.1999.88.1.242

Washburn, D. A., Hopkins, W. D., & Rumbaugh, D. M. (1991). Perceived control in rhesus monkeys (*Macaca mulatta*): Enhanced video-task performance. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*(2), 123–129. doi: 10.1037/0097-7403.17.2.123

CHAPTER 6

Conclusions and recommendations



DISCUSSION

Animal cognition is a well-studied field, with research on animal psychology and cognitive ability growing to over 4000 citations in 2019 alone (Bräuer et al., 2020). Yet, such studies on urban animals remain scarce, despite the evidence for improved cognitive abilities in urban animals (e.g. Liker and Bókony, 2009; Sol et al., 2011; Audet et al., 2016). Through the expansion of urban areas, the establishment of wildlife in environments highly populated by humans may be inevitable for many species. However, those that are unable to adapt and overcome the challenges presented by urbanisation may not become successfully established in these areas (Sih et al., 2011; Sol et al., 2013). An improved understanding of the mechanisms used by wildlife that thrive in urban environments, such as behavioural flexibility, can result in an understanding of the effects of urbanisation on wildlife and may aid in the conservation and management of species in urban settings.

The yellow mongoose is a small carnivore (Do Linh San et al., 2015) that has managed to become established in an urban location where it exploits anthropogenic resources (Cronk and Pillay, 2018, 2019a, 2019b). Although many studies have considered their general ecology (e.g. Nel and Kok, 1999; Cronk and Pillay, 2019a, 2020, 2021) and communication (e.g. le Roux et al., 2008, 2009; Manser et al., 2014), studies on their cognitive abilities had been neglected previously, especially in an urban setting. Similarly, yellow mongooses' diet and food preference has been studied extensively, both in urban and non-urban locations (e.g. Avenant and Nel, 1992; Cavallini and Nel, 1995; Nel and Kok, 1999; Kingdon et al., 2013; Bizani, 2014; Cronk and Pillay, 2018, 2019a, 2019b), yet studies on their decision-making regarding the increased food availability in urban locations are non-existent.

I studied the cognitive abilities of an urban population of yellow mongooses occurring in the Meyersdal Nature Area south of Johannesburg. I considered their learning and problem-solving abilities when presented with a novel problem, and their cognitive flexibility when the learning contingencies changed. I further investigated their response to anthropogenic disturbance, and the effects of such disturbance on their problem-solving, as well as their decision-making when faced with abundant choice. The data from these experiments were collected in the Meyersdal Nature Estate and the Meyersdal Eco Estate, differing in their degree of human contact (Cronk and Pillay, 2018). An additional study site, the Glenvista Renaissance Retirement Village, was included in the initial learning experiment, where mongooses regularly visited residential gardens and even entered houses.

Conducting these studies in the Meyersdal area allowed me to study the cognitive abilities of yellow mongooses in an urban context.

Summary of objectives and findings

The main aim of my study was to assess the cognitive abilities of yellow mongooses, *Cynictis penicillata*, occurring alongside humans in an urban habitat. Cognition entails the perception of environmental cues, processing these cues via learning, storing the learned information in memory, and acting on the learned and stored memories via behaviour and decision-making (Shettleworth, 1998). I explored these components of cognition by assessing (i) whether mongooses were able to learn to solve a novel problem (Chapter 2), (ii) whether mongooses could unlearn previously learned information stored in their memories in favour of learning new information (Chapter 3), (iii) the way in which mongooses processed environmental cues and how their processing mechanisms affected their problem-solving (Chapter 3), (iv) whether mongooses were able to learn to adapt to non-threatening human disturbances and their antipredator decisions (Chapter 4), and (v) to what extent mongooses' decision-making was influenced by an abundance of choice (Chapter 5). These experiments allowed me to explore the cognitive abilities of a generally cryptic, free-living, small carnivore, which cognitive research was previously lacking. Furthermore, the occurrence of these animals in an urban setting allowed me to assess some effects of urban living, and the subsequent human disturbances, on the cognitive ability of urban yellow mongooses.

In the first experimental chapter of this thesis (Chapter 2), I assessed whether urban-dwelling yellow mongooses were able to learn to solve a novel puzzle box problem with increasing complexity. I found that mongooses could learn to solve the puzzle box problem at each stage of complexity, with the problem-solving speed depending on the complexity of the problem (more complex problems required more time to solve). This indicates that mongooses were able to innovate since solving the puzzle box problem required the use of a novel motor action. The mongooses' problem-solving ability differed among the locations, but could not be attributed to differences in levels of neophobia or exploratory behaviour, even though these factors are considered predictors of innovativeness in urban animals (Prasher et al., 2019). Instead, differences in the level of tameness (Seferta et al., 2001) or the degree of disturbances (Kummer and Goodall, 1985) among the urban locations may have contributed to the observed differences in problem-solving efficiency. These results showed

that urban mongooses are innovative, allowing them to solve novel problems and exploit urban food sources.

After finding that mongooses are able to learn to solve novel problems through innovation, I assessed whether they were cognitively flexible (Chapter 3). Firstly, I assessed whether mongooses were capable of reversal learning, an indication of cognitive flexibility in animals (Lucon-Xiccato and Bisazza, 2014; Liu et al., 2016; Izquierdo et al., 2017). The mongooses in my study were capable of both associative and reversal learning. They were more likely to choose the correct box when they made quick decisions, possibly because they used visual and spatial cues. The mongooses also became more efficient at selecting the correct box over time, thereby reducing the time taken to make the correct selection, and increasing the success rate over time. This likely indicates that they learned to use a win-stay, lose-shift strategy (Nowak and Sigmund, 1993; Buechel et al., 2017). Secondly, I assessed whether mongooses experienced divided attention when solving a puzzle box problem in the presence of disturbance. I found that the mongooses successfully solved the puzzle box problem during various levels of distraction, but their problem-solving efficiency declined when there were two or three distractions. This was likely a result of mongooses shifting their attention to and from the puzzle box while remaining vigilant to the distractions. Whether mongooses used divided attention or alternation attention to solve the puzzle box problem, while simultaneously remaining vigilant, is unclear. Still, mongooses were able to focus their attention on two tasks successfully, with their performance only declining during more distractions. The results from the reversal learning experiment, combined with the attention task experiment, indicate that mongooses can adjust their behaviour as their priorities change when dealing with a cognitively demanding task. These results support cognitive flexibility in urban yellow mongooses.

In Chapter 4, I assessed whether yellow mongooses with increased tolerance of humans were able to solve a puzzle box problem faster than those that were more fearful of humans. I expected mongooses occurring in closer proximity to humans to have shorter FIDs, since previous studies had indicated reduced FIDs in areas of increased human disturbance (e.g. Kenney and Knight, 1992; Lord et al., 2001; Webb and Blumstein, 2005; Chapman et al., 2012; McGowan et al., 2014). However, the mongooses in my study had significantly longer FIDs in the location with increased human disturbance compared with the more natural location, even though their FIDs increased with increased proximity to human residents. This likely suggests that the FIDs of mongooses were not related to the level of urbanisation per se, but rather to a combination of factors associated with urban living,

including prior encounters with humans. The mongooses' response to the human disturbance revealed increased fearfulness in those occurring in the more urbanised location (increased distance fled from the box and longer recovery time following the disturbance). However, although there were differences in the level of tolerance of humans, the problem-solving efficiency of mongooses did not differ accordingly. Instead, those with increased tolerance to humans were able to solve the puzzle box problem faster over successive trials. These results demonstrate that the mongooses' level of tolerance of humans does not directly influence their problem-solving ability, but it may affect their ability to respond to human disturbance, which, in turn, may hinder improved problem-solving efficiency if they cannot respond to human disturbance in urban areas.

In the last experimental chapter (Chapter 5), I assessed whether yellow mongooses experienced a paradox of choice, and were, therefore, cognitively challenged when presented with many food choices. Similar to the experiments by Iyengar and Lepper (2000) on humans, the mongooses took longer to choose with the most choice compared with no choice. Furthermore, I found evidence of perseveration when mongooses had more than two choices. The mongooses' decision-making differed between the two locations, with those in the area of lesser human contact experiencing more difficulties with choosing among many options. These results suggest that the mongooses' active decision-making declined with too many choices, possibly due to decision paralysis, and that mongooses were dissatisfied with their decisions resulting in the continuous revisitation of the same bowl. Since the outcome of a paradox of choice includes decision paralysis and dissatisfaction (Schwartz, 2007), there is some indication that the urban mongooses in my study similarly experienced a paradox of choice.

Cognitive abilities of urban-dwelling yellow mongooses

My results provide evidence of well-developed cognitive abilities in yellow mongooses, allowing for (i) learning and innovation aiding in problem-solving during complex novel tasks (Chapter 2), (ii) cognitive flexibility contributing to active adjustment in response behaviour contingent upon environmental cues (Chapter 3), and (iii) adaptation to human presence, allowing for a reduced fear response, faster recovery times, and improved problem-solving efficiency (Chapter 4), but also that (iv) mongooses exhibit cognitive deficits in decision-making during extensive food choice in an urban setting (Chapter 5).

Urban-living mongooses are capable of solving novel problems at varying levels of difficulty (Chapter 2). Johnson-Ulrich et al. (2018) labelled the combination of behavioural traits associated with innovative ability (e.g. high persistence, high motor diversity, exploratory behaviour, high activity, and low neophobia) a "proactive behavioural syndrome". However, the problem-solving ability of yellow mongooses was unrelated to their levels of neophobia, persistence, and exploratory behaviour, and whether they possess this "proactive behavioural syndrome" is unclear. Even so, mongooses exhibited evidence of inhibitory control, the use of novel motor actions, and the ability to extract a general rule, three cognitive factors considered to contribute to innovation (Hauser, 2003; Thornton and Samson, 2012). Not only did these cognitive abilities enable mongooses to innovate and solve a novel problem, but they also further aided cognitive flexibility (Chapter 3). Although persistence is necessary for solving a novel task by not giving up (Thornton and Samson, 2012), consistently performing unrewarding behaviours inhibits problem-solving (Hauser, 1999). Thus, not only was inhibitory control vital in solving the puzzle box task initially (Chapter 2; mongooses reduced the frequency of biting and pawing at the box), but it also contributed to the mongooses' ability to inhibit the learned response of approaching one box when it was no longer rewarding, and instead, they approached the alternative box (Chapter 3). Similarly, once mongooses learned how to open the lid of the puzzle box initially, they were able to apply the same rule to the more complex stages, resulting in improved problem-solving efficiency (Chapter 2). This ability to extract a general rule allowed mongooses to develop a win-stay, lose-shift strategy during the reversal learning task, resulting in fewer errors during successive trials (Chapter 3). Urban-living mongooses thus possess a combination of characteristics necessary for innovation, problem-solving, learning, and cognitive flexibility, possibly aiding in their successful invasion, establishment, and persistence in urban habitats.

Although mongooses are able to exploit urban habitats, the disturbances associated with urban living may challenge mongooses cognitively. The problem-solving ability of mongooses in my study declined with sufficient distraction in both locations (Chapter 3). This was attributed to the animals' limited capacity to process many environmental cues and divide their attention accordingly (Griffiths et al., 2004; Zentall, 2005). The increased disturbance in urban habitats thus requires animals to remain vigilant more often, possibly affecting them negatively, especially when engaged in cognitively demanding tasks. For example, during the initial learning task, mongooses in the Eco Estate took significantly longer to learn to solve the puzzle box problem than those in the Retirement Home (Chapter

2). This difference in problem-solving abilities was attributed to increased disturbance in the Eco Estate, possibly necessitating divided attention, resulting in reduced performance in the puzzle box task. Thus, although urban-adapted species are renowned for their enhanced cognitive abilities (Byrne and Whiten, 1992; Audet et al., 2016), the disturbances linked with urbanisation may be distracting when engaging in cognitively demanding tasks.

The frequent disturbances associated with urbanisation pose another obstacle to urban-living animals. Animals adapted to urban living are often thought to have shorter FIDs, allowing them to flee less frequently during non-threatening disturbances (Møller et al., 2013). However, the mongooses in the more disturbed Eco Estate had significantly longer FIDs than those in the less disturbed Nature Estate, despite their encountering humans more frequently in the Eco Estate (Chapter 4). This supports the finding from Chapter 2 that mongooses in the Eco Estate are quick to flee during a disturbance, often abandoning food in favour of shelter, even if the disturbance was harmless. Such long flight initiation distances are linked with population declines due to the costs of frequent flights perpetuated by urban-linked disturbances (Møller, 2008). Anthropogenic disturbances in urban habitats may, therefore, prohibit access to food resources while encouraging frequent and unnecessary flights, which are costly (Ydenberg and Dill, 1986). Furthermore, habituation to human disturbances was supported by the improved problem-solving in the tolerant mongooses in the Nature Estate, but those fearful of humans in the Eco Estate had no improvement in their problem-solving efficiency, which suggests that urban mongooses may not always be capable of adapting to all possible urban disturbances.

Many studies have considered how the various characteristics of urban environments impact animals, resulting in animals either thriving in an urban landscape or failing to adapt entirely (Sih et al., 2011; Sol et al., 2013). While disturbances caused by humans and their general activities threaten urban animals (McKinney, 2002, 2006), features such as increased food availability and reduced predation risk are thought to positively influence animals' successful adaptations to urban living (Møller, 2012). However, the impact of these environmental changes on animals' cognition is not usually known. The mongooses in my study were cognitively challenged when faced with an extensive selection of food choices (Chapter 5). This was possibly the result of cognitive overload when having to process too much information during a cognitive task involving decision-making, resulting in a paradox of choice. This was exhibited by increased decision time with many choices. The mongooses in the Eco Estate may instead have used a satisficing strategy, whereby cognitive overload is avoided during extensive choice scenarios by simply choosing any acceptable option. The

limited cognitive load of animals restricts the optimal processing of many cues, which may explain why the mongooses in my study experienced the paradox of choice. Although selective attention may reduce the probability of experiencing cognitive overload (Commodari, 2017), it may not be a feasible strategy in an urban environment, considering the effects of human disturbances on animal cognition and the abundance of available choices. However, dividing attention among many cues is cognitively demanding (Griffiths et al., 2004; Zentall, 2005). This supports the idea that the mongooses in my study may instead have used alternating attention to successfully engage with a cognitively demanding task during significant distraction (Chapter 3). The mongooses in my study may thus have adopted relevant strategies of avoiding cognitive overload whilst having to engage with cognitive tasks associated with navigating an urban landscape, especially in areas with increased human disturbance.

Overall, the distinct levels of human presence and disturbance in the locations in my study affected the various components of mongoose cognition and behaviour differently. When comparing the two Meyersdal estates exclusively (the results from the Retirement Home could not be compared among the various experiments), mongooses' neophobia (Chapter 2), FID (Chapter 4), and decision-making (Chapter 5) were influenced by location, but their problem-solving (Chapter 2) and cognitive flexibility (Chapter 3) were not. This observation may point toward urban-induced behavioural adaptations in urban mongooses, especially such behavioural changes associated with tolerance of humans and human-linked disturbances, whereas no comparable urban-induced cognitive adaptations were observed. These results bear important implications for future studies considering behavioural modifications in urban-adapted animals, particularly those concerned with cognitive adaptations.

CONCLUSIONS

I considered cognition in an urban population of yellow mongooses. I conducted five experiments, each investigating a component of cognition in an urban context. These experiments explored mongooses learning, problem-solving, and cognitive flexibility, likely contributing to their successful urban adaptation. Furthermore, I studied the effects of urbanisation on their cognitive abilities, including the effects of direct human disturbances and increased food availability associated with urban living. The cognitive abilities of yellow mongooses have not been studied before, particularly in a free-living urban population.

My study showed that yellow mongooses could learn to solve a novel problem to obtain a food incentive and continue to solve the problem even when the complexity increases. Furthermore, mongooses are capable of devising innovative solutions to complex problems. This is beneficial for urban living since the ability to solve novel problems through innovation may allow animals to exploit anthropogenic resources such as food and nesting sites. Furthermore, mongooses can behave flexibly when engaging in cognitively demanding tasks, allowing them to adjust their behaviour to more appropriate behaviours when necessary. This cognitive flexibility likely allows them to persist in urban locations where environmental changes occur rapidly, demanding rapid behavioural changes in urban-living species. I additionally showed that mongooses vary in their level of tolerance of humans, which may be related to a number of urban-linked disturbances or previous experiences with humans. The difference in tolerance of humans may affect mongooses' antipredator behaviour and stress responses, although it appears to bear no direct influence on their cognitive abilities other than inhibiting improved problem-solving, likely related to an inability to adapt to the disturbance in fearful mongooses. Finally, urban-living mongooses may not benefit from the increased food availability in urban areas, since the increased choice associated with increased food availability may be cognitively challenging. However, mongooses may have adopted survival strategies allowing them to overcome cognitive challenges in urban areas.

My study was the first to address the cognitive abilities of free-living yellow mongooses in an urban setting. The use of innovation, problem-solving, and adaptation to the presence of humans, combined with their ability to exploit anthropogenic food sources, might contribute to urban mongooses continuing to survive in heavily altered urban environments. Despite the challenges associated with human disturbance, yellow mongooses have shown cognitive skills allowing them to overcome novel obstacles. It is likely that the mongooses' ability to engage in cognitive tasks is characteristic of generalist mesocarnivores (e.g. Sol et al., 2016, Stanton et al., 2021), but it could further be linked with their affinity for urban areas. Whether my results are consistent among yellow mongooses generally is presently unknown. Conducting additional analyses on non-urban mongooses is necessary to reveal whether mongooses have pre-existing abilities allowing them to succeed with the spread of urbanisation. If not, we may conclude that only those with the ability to learn to solve complex problems are able to exploit urban areas. The results from my study provide insight into the effects of animal cognition on urban living, and the effects of urbanisation on animal cognition. An improved understanding of cognition in urban animals may allow for reduced

human-wildlife conflict while minimising the effects of urbanisation on urban animals, allowing for the coexistence of humans and wildlife.

FUTURE DIRECTIONS

My study showed that urban mongooses have the cognitive ability to engage with novel and complex tasks that may have aided their successful establishment and continued survival in urban areas. However, whether these cognitive abilities are characteristic of yellow mongooses generally, or are unique to urban-dwelling mongooses, is unknown. A comparative study incorporating a non-urban population will be valuable in discerning the impacts of urbanisation versus inherent cognitive abilities in yellow mongooses. Very few comparative studies within areas of differing levels of urbanisation exist (Papp et al., 2015). Thus far, the available literature suggests that individuals occurring in areas of higher urbanisation are better problem-solvers/innovators (Liker and Bókony, 2009; Sol et al., 2011; Audet et al., 2016). Such a comparative study will especially be useful for improving our understanding of the urban exploitation of animals. For example, were mongooses able to establish an urban population because they were preadapted for urban living, or were they able to rapidly adapt to the challenges of living in an urban location? Animals in urban areas either undergo selection so that those with the traits necessary for urban living survive and persist in urban areas (natural selection), or individuals that already have the necessary traits are able to move into the urban areas successfully (preadaptation; non-random sorting; Goumas et al., 2020). While some researchers believe that animals adjust their behaviour to suit their habitat (behavioural plasticity; Sol et al., 2013; Goumas et al., 2020), others believe that microevolutionary changes are responsible for the behavioural differences observed in animals living alongside humans (Møller et al., 2013; Vrbanec et al., 2021). Of course, the possibility exists that a combination of both is true: animals with beneficial traits for urban living, shaped by their previous environment, may become established in urban environments and undergo additional adaptations via phenotypic plasticity (Price et al., 2003; Sih et al., 2011). For example, animals with short FIDs in the original, rural population were likely more successful at invading urban habitats, after which FIDs became more variable as the animals adapted to the new environment (Møller, 2010).

A potential caveat with urban-rural comparisons is discerning actual urban effects from other confounding factors. For example, a non-urban population may have improved cognitive abilities compared with an urban population, not necessarily because of the effects

of urbanisation acting on the urban population, such as increased disturbance, but instead as a result of conditions such as improved motivation to feed due to malnourishment (Fernández-Juricic et al., 2002). The ability to capture, mark, and recapture individual mongooses may thus be valuable in understanding the effects of body condition on their cognitive abilities. Additionally, the marking of individual mongooses may further contribute to understanding how age, social rank, sex, and personality affect the cognitive abilities of urban yellow mongooses.

REFERENCES

Audet, J. N., Ducatez, S., & Lefebvre, L. (2016). The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, *27*(2), 637–644. doi: 10.1093/beheco/arv201

Bräuer, J., Hanus, D., Pika, S., Gray, R., & Uomini, N. (2020). Old and new approaches to animal cognition: There is not "one cognition." *Journal of Intelligence*, *8*(3), 28. doi: 10.3390/jintelligence8030028

Buechel, S. D., Boussard, A., Kotrschal, A., van der Bijl, W., & Kolm, N. (2017). Brain size affects performance in a reversal-learning test. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1871), 20172031. doi: 10.1098/rspb.2017.2031

Byrne, R. W., & Whiten, A. (1992). Cognitive Evolution in Primates: Evidence from Tactical Deception. *Man*, *27*(3), 609. doi: 10.2307/2803931

Chapman, T., Rymer, T., & Pillay, N. (2012). Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris*. *Naturwissenschaften*, *99*(11), 893–902. doi: 10.1007/s00114-012-0971-8

Commodari, E. (2017). Novice Readers: The role of focused, selective, distributed and alternating attention at the first year of the academic curriculum. *I-Perception*, *8*(4), 204166951771855. doi: 10.1177/2041669517718557

Cronk, N. E., & Pillay, N. (2018). Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethologica*, *21*(2), 127–136. doi: 10.1007/s10211-018-0291-x

Cronk, N. E., & Pillay, N. (2019a). Flexible use of urban resources by the yellow mongoose *Cynictis penicillata*. *Animals*, *9*(7), 447. doi: 10.3390/ani9070447

Cronk, N. E., & Pillay, N. (2020). Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment. *Journal of Urban Ecology*, *6*(1), 1–9. doi: 10.1093/jue/juaa013

Cronk, N. E., & Pillay, N. (2021). Home range and use of residential gardens by yellow mongoose *Cynictis penicillata* in an urban environment. *Urban Ecosystems*, *24*(1), 127–139. doi: 10.1007/s11252-020-01022-1

Cronk, N., & Pillay, N. (2019b). Dietary overlap of two sympatric African mongoose species in an urban environment. *Mammalia*, *85*(5), 428–438. doi: 10.1515/mammalia-2018-0113

Do Linh San, E., Cavallini, P., & Taylor, P. (2015). *The IUCN Red List of Threatened Species 2015* [Data set]. International Union for Conservation of Nature. doi: 10.2305/IUCN.UK.2015-4.RLTS.T41597A45205726.en

Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, *80*(7), 1212–1220. doi: 10.1139/z02-104

Goumas, M., Lee, V. E., Boogert, N. J., Kelley, L. A., & Thornton, A. (2020). The role of animal cognition in human-wildlife interactions. *Frontiers in Psychology*, *11*, 589978. doi: 10.3389/fpsyg.2020.589978

Griffiths, S. W., Brockmark, S., Höjesjö, J., & Johnsson, J. I. (2004). Coping with divided attention: The advantage of familiarity. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1540), 695–699. doi: 10.1098/rspb.2003.2648

Hauser, M. D. (1999). Perseveration, inhibition and the prefrontal cortex: A new look. *Current Opinion in Neurobiology*, *9*(2), 214–222. doi: 10.1016/S0959-4388(99)80030-0

Hauser, M. D. (2003). To Innovate or Not to Innovate? That is the question. In S. M. Reader & K. N. Laland (Eds.), *Animal innovation* (pp. 329–338). Oxford ; New York: Oxford University Press.

Iyengar, S. S., & Lepper, M. R. (2000). When choice is demotivating: Can one desire too much of a good thing? *Journal of Personality and Social Psychology*, *79*(6), 995–1006. doi: 10.1037/0022-3514.79.6.995

Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H., & Holmes, A. (2017). The neural basis of reversal learning: An updated perspective. *Neuroscience*, *345*, 12–26. doi: 10.1016/j.neuroscience.2016.03.021

Johnson-Ulrich, L., Johnson-Ulrich, Z., & Holekamp, K. (2018). Proactive behavior, but not inhibitory control, predicts repeated innovation by spotted hyenas tested with a multi-access box. *Animal Cognition*, *21*(3), 379–392. doi: 10.1007/s10071-018-1174-2

Kenney, S. P., & Knight, R. L. (1992). Flight distances of black-billed magpies in different regimes of human density and persecution. *The Condor*, *94*(2), 545–547. doi: 10.2307/1369231

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *308*(1135), 203–214. doi: 10.1098/rstb.1985.0020

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behaviour*, *75*(3), 943–949. doi: 10.1016/j.anbehav.2007.07.014

Le Roux, A., Cherry, M. I., & Manser, M. B. (2009). The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality. *Naturwissenschaften*, *96*(5), 575–584. doi: 10.1007/s00114-008-0506-5

Liker, A., & Bókony, V. (2009). Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences*, *106*(19), 7893–7898. doi: 10.1073/pnas.0900042106

Liu, Y., Day, L. B., Summers, K., & Burmeister, S. S. (2016). Learning to learn: Advanced behavioural flexibility in a poison frog. *Animal Behaviour*, *111*, 167–172. doi: 10.1016/j.anbehav.2015.10.018

Lord, A., Waas, J. R., Innes, J., & Whittingham, M. J. (2001). Effects of human approaches to nests of northern New Zealand dotterels. *Biological Conservation*, *98*(2), 233–240. doi: 10.1016/S0006-3207(00)00158-0

Lucon-Xiccato, T., & Bisazza, A. (2014). Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biology Letters*, *10*(6), 20140206. doi: 10.1098/rsbl.2014.0206

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal Complexity in Meerkats and Other Mongoose Species. *Advances in the Study of Behavior*, *46*, 281–310. doi: 10.1016/B978-0-12-800286-5.00006-7

McGowan, M. M., Patel, P. D., Stroh, J. D., & Blumstein, D. T. (2014). The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. *Ethology*, *120*(11), 1081–1089. doi: 10.1111/eth.12281

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience*, *52*(10), 883–890. doi: 10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. doi: 10.1016/j.biocon.2005.09.005

Møller, A. P. (2008). Flight distance and population trends in European breeding birds. *Behavioral Ecology*, *19*(6), 1095–1102. doi: 10.1093/beheco/arn103

Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology*, *21*(2), 365–371. doi: 10.1093/beheco/arp199

Møller, A. P. (2012). Reproductive behaviour. In U. Candolin & B. B. M. Wong (Eds.), *Behavioural Responses to a Changing World* (pp. 106–118). Oxford University Press. doi: 10.1093/acprof:osobl/9780199602568.003.0008

Møller, A. P., Grim, T., Ibanez-Alamo, J. D., Marko, G., & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, *24*(5), 1211–1217. doi: 10.1093/beheco/art054

Nel, J. A. J., & Kok, O. B. (1999). Diet and foraging group size in the yellow mongoose: A comparison with the suricate and the bat-eared fox. *Ethology Ecology & Evolution*, *11*(1), 25–34. doi: 10.1080/08927014.1999.9522839

Nowak, M., & Sigmund, K. (1993). A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature*, *364*(6432), 56–58. doi: 10.1038/364056a0

Papp, S., Vincze, E., Preiszner, B., Liker, A., & Bókony, V. (2015). A comparison of problem-solving success between urban and rural house sparrows. *Behavioral Ecology and Sociobiology*, *69*(3), 471–480. doi: 10.1007/s00265-014-1859-8

Prasher, S., Evans, J. C., Thompson, M. J., & Morand-Ferron, J. (2019). Characterizing innovators: Ecological and individual predictors of problem-solving performance. *PLOS ONE*, *14*(6), e0217464. doi: 10.1371/journal.pone.0217464

Price, T. D., Qvarnström, A., & Irwin, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1523), 1433–1440. doi: 10.1098/rspb.2003.2372

Schwartz, B. (2007). *The paradox of choice: Why more is less* (Reissued). New York, NY: Harper Perennial.

Seferta, A., Guay, P.-J., Marzinotto, E., & Lefebvre, L. (2001). Learning differences between feral pigeons and zenaida doves: The role of neophobia and human proximity. *Ethology*, *107*, 281–293. doi: 10.1046/j.1439-0310.2001.00658.x

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change: Behaviour and evolution. *Evolutionary Applications*, *4*(2), 367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS ONE*, *6*(5), e19535. doi: 10.1371/journal.pone.0019535

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Sol, D., Sayol, F., Ducatez, S., & Lefebvre, L. (2016). The life-history basis of behavioural innovations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150187. doi: 10.1098/rstb.2015.0187

Stanton, L. A., Bridge, E. S., Huizinga, J., Johnson, S. R., Young, J. K., & Benson-Amram, S. (2021). Variation in reversal learning by three generalist mesocarnivores. *Animal Cognition*, *24*(3), 555–568. doi: 10.1007/s10071-020-01438-4

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468. doi: 10.1016/j.anbehav.2012.03.018

Vrbanec, L., Matijević, V., & Guenther, A. (2021). Enhanced problem-solving ability as an adaptation to urban environments in house mice. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1945), 20202504. doi: 10.1098/rspb.2020.2504

Webb, N. V., & Blumstein, D. T. (2005). Variation in human disturbance differentially affects predation risk assessment in Western gulls. *The Condor*, *107*(1), 178–181. doi: 10.1093/condor/107.1.178

Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. *Advances in the Study of Behavior*, *16*, 229–249. doi: 10.1016/S0065-3454(08)60192-8

Zentall, T. R. (2005). Selective and divided attention in animals. *Behavioural Processes*, *69*(1), 1–15. doi: 10.1016/j.beproc.2005.01.004