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Decision-making during problem-solving and innovation in an urban dwelling population of yellow mongooses (Cynictis penicillata)

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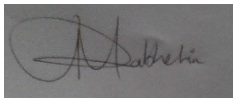


Muneera Dabhelia

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Master of Science.
Johannesburg, 2022

Declaration

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



Muneera Dabhelia

Date: 13/06/2022

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Abstract

The rapid exponential growth of towns and cities has impacted wildlife in various ways, causing the decline and redistribution of species. Yet, some wild animal species have established themselves in urban environments through behavioural modifications. Urban-adapted animals are presumed to have advanced cognitive abilities and are behaviourally flexible in terms of their decision-making processes when faced with a novel problem. Decision-making in urban animals has not been extensively. I studied decision-making in two populations urban of yellow mongooses (*Cynictis penicillata*) using a problem-solving task that increased in complexity. The behaviours of the mongoose while interacting with a novel object was analysed using three levels of interpretation. The mongooses were studied in areas of varying human disturbance (a Nature Estate where wildlife was located away from human residents and an Eco Estate where mongooses had regular close contact with people), south of Johannesburg, South Africa. I used a single-access puzzle box with a hinged lid, containing a food incentive to record the general behaviour and decision making of the yellow mongooses to open the box and gain access to the food incentive. The experiment comprised of four stages in sequential order on different days, starting with an open puzzle box with food (stage 1), to a closed box propped open with a stick (stage 2), to a closed box (stage 3), and finally a closed box with an impediment on the lid (stage 4). Ten sites (1 mongoose per site) were sampled repeatedly for several trials (5 to 9) for each stage. From camera trap footage, I assessed how long it took the mongooses to open the box (latency of completion) in each stage of complexity, the frequency of behaviours, how often each behaviour followed another (behavioural transitions) while the mongooses were interacting with the puzzle box and the spontaneous alternation behaviour score (SAB score) to analysis the moment-to-moment change in behaviours. The latency to consume the food incentive was lowest in stage 1, increased in subsequent stages and was faster in the Eco Estate compared to the Nature Estate. Eight behaviours were recorded: biting, sniffing, pawing, pulling, pushing the puzzle box, digging around or underneath the box, locomotion around the puzzle box, and vigilance. The frequency of three behaviours - digging, investigating and vigilance was summed – to account for the small sample sizes. The frequency of digging and the frequency of vigilance was lowest in stage 1 compared to subsequent stages. The frequency of investigating was highest in stages 1 and 2 and decreased in stages 3 and 4. Location did not significantly predict the frequency of digging, although the frequency of investigating and vigilance was higher in the Eco Estate compared to the Nature Estate. For the behavioural

transitions and SAB scores, all eight behaviours were analysed. The number of significant behavioural transitions increased as the level of complexity of the task increased. The number of significant transitions in stage 2 and stage 3 in the Eco Estate was greater compared to the Nature Estate, but in stage 4 the number of significant transitions was greater in the Nature Estate compared to the Eco Estate. The SAB score for stage 2 did not significantly differ from stage 3. However, the SAB score for stage 3 were significantly lower compared to those of stage 4. The SAB score in the Eco Estate was significantly higher than the Nature Estate. My findings indicate that the yellow mongooses were able to modify their decision-making strategies by selecting behaviours that were most appropriate to solving the problem and rejecting ones that did not, particularly at greater stages of complexity of the task. In addition, mongooses in the Eco Estate, where they encounter people more often, made less accurate moment to moment decisions and took longer to solve the puzzle box tasks compared to the mongooses in the Nature Estate. Such flexibility in decision-making likely enables the yellow mongooses to thrive in human-impacted environments.

Keywords: *Behavioural transitions, decision making, puzzle box, SAB score, urbanization, yellow mongoose*

Introduction

Urbanisation

Urbanisation is thought to be one of the greatest dangers to biodiversity in recent decades (Łopucki and Kitowski, 2017). Artificial structures, such as buildings, roads, gardens, dump sites and parklands are displacing the natural environment, affecting wildlife in a variety of ways (Bateman and Fleming, 2012). Many free-living species are experiencing habitat loss, habitat fragmentation, and pollution (such as light and air pollution) as a result of urbanisation, processes that is being exacerbated by climate change (McKinney, 2002; 2006). In addition, conflicts such as increased human-wildlife conflict (wildlife being hunted and/or prosecuted; Goumas *et al*., 2020), high densities of exotic predators (e.g., domestic cats and dogs), foreign parasites, and road deaths are common (Møller, 2008). As a result, urbanisation may cause a decline in species richness and range-shifts in the distribution of wildlife (Sol *et al.,* 2013). For example, artificial lights in cities cause a reduction in sea turtle survival rates by disrupting the nocturnal orientation of sea turtle hatchlings (*Caretta caretta* and *Chelonia mydas)* as they crawl from their nest to the ocean (Tuxbury and Salmon, 2005). Furthermore, animals such as moose (*Alces alces*) and black bears *(Ursus americanus)*, which cannot cope with human induced changes, have much smaller home ranges in urban environments compared to their home range size in a natural environment (meta-analysis in O'Donnell and del Barco-Trillo, 2020). Conversely, urban areas tend to have a warmer microclimate, lack of apex predators, and an increase in anthropogenic food sources (Partecke *et al.*, 2006), allowing certain animals such as urban adaptors or urban exploiters to thrive.

Rapid changes brought about by urbanisation expose animals to novel selection pressures that affect an individual's ability to survive and reproduce, and ultimately affects the survival of future generations (Lowry *et al.*, 2013). For an animal to survive rapid environmental change, it should be able to track these changes and respond accordingly (Sih *et al.*, 2010; 2011). There are several well-known wild species that successfully exploit urban areas, such as ground squirrels (*Xerus inauris*; Chapman *et al*., 2012), moles (*Talpidae*), raccoons (*Procyon lotor*), foxes (*Vulpes* spp.) and coyotes (*Canis latrans*) (McCleery, 2010). These species are known as urban "adaptors" or "exploiters"; urban adaptors live permanently in human-altered landscapes or make brief forays into such landscapes and urban exploiters depend on human provided resources for food and shelter (Lowry *et al*., 2013). These animals have learnt to exploit urban areas by feeding on anthropogenic food sources,

benefitting from reduced predation risk, and thriving in the warmer microclimate (Bateman and Flemming, 2012). In contrast, species that are characterized by a low fear tolerance of unfamiliar objects, rapid and strong cortisol responses, and long flight initiation distances (i.e., fleeing from people at larger distances) are more likely to be sensitive to environmental change and tend to avoid urban environments and depend exclusively on natural resources (Rebolo-Ifrán *et al*., 2015); these are known as urban "avoiders". For example, several small bodied European and Australian birds tend to be urban avoiders and are less likely to move into human-impacted areas since they are fearful of humans, which is evident by their long flight initiation distances when approached by people (reviewed in Samia *et al.*, 2015). Additionally, large animals, such as bison (*Bison bison*), elk (*Cervus canadensis*) and bears (*Urus* spp.) tend to avoid urban areas and rely solely on naturally occurring resources (McCleery, 2015).

The mechanisms that enable some species to adapt to urban areas have been studied in the past decade or so (Sih *et al*., 2011; Sol *et al*., 2013). Animals with appropriate life history traits (e.g., small body size, short generational times, higher reproductive output), generalist diets and/or displaying behavioural flexibility (i.e., the ability to adjust behaviours in response to environmental changes) are key mechanisms enabling wild animals to cope in rapidly changing environments (Sol *et al*., 2013).

Cognition and behavioural flexibility

Behavioural flexibility may occur through an immediate change in behaviour, (usually through learning) in response to environmental change (Sol *et al*., 2013). Prey species can respond to predation risk during foraging in various ways. (i) Trading-off foraging behaviours for vigilance, for example, free-ranging black-capped chickadees (*Parus atricapillus*) change their foraging strategy and become more vigilant when foraging in a high-predation area (Lima, 1985). (ii) Modifying foraging behaviours from previously learnt experiences to reduce the risk of predation. Honeybees (*Apis* spp), for example, avoid flowers that potentially harbour predacious spiders by adopting changes in flight behaviour such as flying slower over the flowers and or scanning the flower twice as long to detect a potential predator before landing on a particular flower (Yokoi and Fujisaki, 2009). (iii) Prey species develop new predator-avoidance behaviours and continue to forage (Sol *et al*., 2013). For instance, the Japanese majid crab (*Tiarinia cornigera*) modifies its antipredator behaviour (Thanh *et al.*, 2003) by adjusting the composition of algae on its shell, thereby altering the degree of camouflage (Thanh *et al.*, 2003).

Urban exploiters and adaptors change their behaviours in response to human disturbances (Sol *et al*., 2013). For example, coyotes (*Canis latrans*) switch their activity patterns from diurnal to nocturnal to avoid or reduce human encounters, resulting in reduced collisions with vehicles and decreased human wildlife conflict (Gehrt, 2007). Species with the ability to acquire new information from the environment, retain this information, and modify their behaviour based on previously acquired information, display innovative and modified behavioural responses (Dugatkin, 2004). It has been proposed that behavioural modification through learning is a key aspect in allowing animals to exploit human-impacted areas (Wang and Candolin, 2015; Sih, 2013; Sih *et al*., 2011; Sol *et al*., 2011). For example, Keas (*Nestor notabilis*) in New Zealand (Gajdon *et al*., 2006) have learned to open trash cans and feed on anthropogenic food sources. This resulted in the implementation of "animal-proof" dustbins, which had locks on the lid. However, Keas have learned that by knocking the dustbin over the locks break open. Should the lock not break on the initial attempt, the Keas would persist until they found an alternate solution- using previously learned information (Ramsey *et al.*, 2007), to open the dustbin to obtain the required food source. Thus, illustrating its learning and problem-solving capabilities.

The ability of an animal to modify its behavioural responses to its immediate environment may be attributed to their learning abilities and cognition (Dukas, 2004; Dugatkin, 2004; Sol *et al.,* 2013). Cognition is the ability of an animal to acquire new information through perception or past experiences, process this information through learning, store the newly acquired information in their memory, and then appropriately modify their behaviour through decision-making based on the newly acquired information (Shettleworth, 1998). Cognition is an essential mechanism for problem-solving and innovation (defined as an individual's ability to apply previously learnt techniques to a novel problem; Kummer and Goodall, 1985; Reader and Laland, 2003). Without evidence of learning, behavioural responses or modification can be considered accidental or improvised (Reader and Laland, 2003; Ramsey *et al*., 2007). However, cognition has costs such as a high energy demand to fuel brain tissues and the development of new neural networks because of learning (Kandel and Hawkins, 1992). Therefore, it has been proposed that animals with large brains relative to their body size are capable of enhanced problem-solving and cognitive abilities which allow for flexible behavioural responses (the cognitive buffer hypothesis; Sol *et al.*, 2013). For instance, the New Caledonian crow (*Corvus moneduloides*) does not interpret and respond to novel problems in a predefined manner. Instead, it generates innovative solutions to novel problems (Bluff, 2006). In novel extraction tasks, these crows

can make tools, learn to use the tools and use complex methods while ignoring or rejecting methods that are ineffective to acquire food or other desirable items (Auersperg *et al.,* 2011; Jelbert *et al.*, 2015). The crow's capacity to recognize which methods work, as well as its ability to plan and follow a sequence of problem-solving actions, may indicate an enhanced cognitive capacity (Jelbert *et al.*, 2015).

Species that are capable of innovation in rapidly changing areas can alter their behavioural responses to match environmental demands (Daniels *et al.*, 2019). Urban adaptors are therefore more behaviourally flexible compared to their naturally occurring counterparts (Audet *et al.*, 2016; Chow *et al*., 2021). Animals acquire new information in response to changes in the environment and can solve novel problems which they would not have been able to solve if they were in a homogeneous environment (Hendry *et al.*, 2008). Chow *et al*. (2021) tested problem-solving and innovation in eastern grey squirrels (*Sciurus carolinensis*) using a food extraction task with two levels of complexity and found that the squirrels were able to adjust their behaviours in each stage of complexity to access the food incentive (Chow *et al.*, 2021). Additionally, Chow *et al*., (2021) found that the urban population was better at solving problems compared to their rural counterparts. The ability of an animal to learn and change their behaviour in response to environmental changes is essential for survival in a rapidly changing environment (Lee and Thornton, 2021). Furthermore, Sol *et al.,* (2009) suggests that animal that are behaviourally flexible in terms of innovation and problem solving can buffer the negative effects of urbanisation (i.e., The Cognitive Buffer Hypothesis).

Cognition is further defined as the conscious awareness and understanding of spatial information about an animal's immediate environment (Shettleworth, 1998), which allows for more flexible behavioural responses in decision-making processes (Ten Berge and Van Hezewijk, 1999). For example, in a hypothetical feeding experiment in which pushing a green handle provides a food reward, an individual requires the ability to discriminate between different colours, associate the green handle with a reward, remember this association, and recall it in the next encounter (Mazza *et al*., 2018). How the individual focuses its attention (termed its cognitive style) may influence its performance (Sih and Del Giudice, 2012). For instance, one individual may continue to push the green handle to obtain a reward while ignoring other cues that could indicate a reward, while another individual may continue to sample the surroundings, pushing other handles (Bebus *et al*., 2016). The individual that consistently pushes the green handle may not be changing its decision-making process to solve the problem and continues performing the same behaviour despite receiving

no reward. In contrast, the second individual may be more flexible in its decision-making and be able to alter its behaviour to arrive at a better solution (Mazza *et al*., 2018; Bebus *et al*., 2016).

Decision-making

To make optimal decisions, an animal must identify and select the specific behavioural or cognitive options from numerous alternatives (Budaev, *et al*., 2019). This requires the integration of sensory inputs and the consideration of conflicting needs (Mangel and Clark, 1986; McNamara and Houston, 1986). Animals are constantly making decisions about which mate to choose (Bateson, 1983), where to live (Partridge, 1978) and forage (Stephens and Krebs, 1986), and whether to engage in activities that may expose them to danger (Lima and Dill, 1990; Fawcett *et al.*, 2013). The result of these decisions may influence the survival of the animal, i.e., how long it will live for, the number of offspring it may produce, and its access to food (Blumstein and Bouskila, 1996). Decision-making strategies in free-living animals can often be interpreted as the product of selective pressures that favour behaviours that are efficient and effective (Marsh, 2002). The prevailing environment and social context of an animal are important in influencing the decision-making because decisions are based on context (Owen, *et al*., 2017). Behavioural strategies in decision-making, such as constantly gathering and processing information about the environment, creates energetic costs (Brewer and Stern, 2005). Therefore, it is often easier to use previously learned patterns to make decisions that have a greater adaptive value when situations are similar (Marsh, 2002). However, in constantly changing environments where food availability may be unpredictable (e.g., in winter), previously learnt information about food sources may have low adaptive value (Rochais *et al*., 2019). For example, African striped mice (*Rhabdomys pumilio*) occur in environments such as the Succulent Karoo and grasslands where food availability is affected by seasonal changes. African striped mice experience low food availability in the hot dry summer months and high food availability in the wet winter months in the Succulent Karoo; Schradin and Pillay, 2005). African striped mice cope with changes in food availability by modifying their problem-solving abilities such as where to start searching, how long to search for, and whether or not to feed on novel food sources (i.e., cognitive resilience; Rochais *et al*., 2019). The ability to adjust decision-making (e.g., during foraging) depends on an animal's capacity to recall information such as potential food sites, locate the optimal foraging sites, and decide when to forage at these sites

(Tinbergen, 1981; Cuthill and Kacelnik, 1990). However, when a decision is made the outcome is often uncertain and the animal must be able to modify its behaviour to achieve the optimal outcome (Budaev *et al*., 2019).

The ability of animals to learn from previous experiences and modify their behaviour to best suit its immediate needs (Raine and Chittka, 2012) has been proposed as one of the mechanisms underlying decision-making abilities in various ecological contexts, such as in rapidly changing environments (Fawcett *et al.,* 2014). Urban adapters cope with rapidly changing environments by modifying their decision-making to suit their immediate environment (Lee and Thornton, 2021). For example, as *Temnothorax* ants nest in friable rock crevices, colonies often face the challenge of finding new homes (Chittka *et al*., 2009). In harsh conditions (such as in winter), these ants are less discriminating and usually select nest sites more quickly than they do during more favourable conditions (Franks *et al*., 2003). Various studies have considered decision-making (Blumstein and Bouskila, 1996; Chittka *et al*., 2009; Budaev *et al*., 2019) yet very few have considered it during problem-solving in an urban setting.

Decision-making is often tested in a laboratory, and usually involves binary choices which lack ambiguity for the test animal (e.g., left-right or blue-red binary choices) (Staddon, 2016). This approach tends to force the animal to make one of two choices, reducing the number of possible outcomes that would be found under natural conditions (Yoo *et al.,* 2021). This reductive approach misses crucial aspects of the decision-making process, such as what led the animal to make that choice, i.e., its physiological state (e.g., hunger) or the environmental conditions (Budaev *et al*., 2019). The choices made by a test animal in a controlled setting happen instantaneously or irrespective of time, and once the choice is made, it is usually irreversible (Budaev *et al*., 2019). However, decisions in the natural world are not as discrete and should rather be viewed as a continuum of behavioural adjustments leading to the final choice (Yoo *et al.,* 2021). When a widow-skimmer dragonfly (*Libellula luctuosa*) stalks its prey, for example, it must continuously monitor the position of its prey, since both prey and predator move quickly through a three-dimensional space (Gonzalo-Bellido *et al*., 2016). These dragonflies cannot make discrete decisions since the possibilities of obtaining the prey keeps changing. Instead, they must continuously respond to the prey's behaviours (Kohn *et al*., 2018). The dragonfly does this by repositioning its body to track and predict the prey's next position and calculate an intercept-route (Gonzalo-Bellido *et al.*, 2016). Each behavioural change emerges from a wide range of possibilities, in which each behavioural response follows from the previous response. Therefore, considering decision-

making on a moment-to-moment basis, including the entire process leading up to the outcome, will provide a holistic understanding of how the animal is solving a problem (Yoo *et al.*, 2021).

The Yellow Mongoose

The yellow mongoose (*Cynictis penicillata*) is a small meso-carnivore of the Herpestidae family. Yellow mongooses are widespread throughout South Africa, Namibia and Lesotho, and can be found in habitats such as semi-arid grasslands, savannas and shrublands (Kingdon *et al*., 2013). Yellow mongooses grow up to 0.5 m in length and weigh approximately 1 kg as a fully grown adult (Do Linh San *et al*., 2015). They have a reddish-yellow coat, a triangular face with a pointed snout and a distinguishable bushy, white-tipped tail (Skinner and Chimimba, 2005). Yellow mongooses live in small groups consisting of 8 to 10 juveniles, sub-adults, and adults that occupy underground burrows (Ngalo, 2014). However, yellow mongooses usually forage alone (le Roux *et al.*, 2009). They are primarily diurnal, and most active between 06h00-12h00 and 16h00-17h00 (Cronk and Pillay, 2019).

Yellow mongooses are generalists that feed mostly on insects and carrion (Kingdon *et al*., 2013). In a food choice experiment in which, urban yellow mongooses were presented with a choice of dog kibble, deli meat offcuts, bread, chicken eggs and insects. The urban yellow mongoose preferred deli meats compared to the other choices, including more natural food sources such as insects in summer (Cronk and Pillay, 2018). In the winter months, however, mongooses preferred to feed on natural food sources, and do so for longer durations than in summer (Cronk and Pillay, 2018). In addition, mongooses are quick to approach feeding stations and display reduced vigilance, indicating that the mongooses are habituated to urban areas and the general lack of predators (Cronk and Pillay, 2018). The yellow mongooses are thriving in urban environments (Cronk and Pillay, 2018; 2019) but thus far however no studies have looked at the behavioural flexibility or cognitive abilities of the yellow mongoose.

Aims, objectives and predictions

The aim of my study was to analyse decision-making during problem-solving and innovation in urban-dwelling yellow mongoose (*Cynictis penicillata*) in two populations with differing levels of anthropogenic disturbance. I used a puzzle box to assess whether the yellow mongooses could learn to access a food incentive. The puzzle boxes were set up close to yellow mongoose colonies in two areas in an urban estate with differing levels of

anthropogenic disturbance. My experiments were designed to train the mongooses to access and then engage with the devices through four stages (with increasing complexity) to access a food incentive.

To analyse decision making during problem solving of urban yellow mongoose the behaviours while interacting with the puzzle box was analysed on three levels of interpretation which follows as; the frequency of behaviours, behavioural patterns and the spontaneous alternation score (as discussed below).

My first objective was to record the latency of the mongoose to obtain the food incentive and to analyse the frequency of behaviours that the yellow mongooses displayed at each stage of complexity. The second objective was to analyse the moment-by-moment decision-making by the mongooses at each stage of complexity of the puzzle box by analysing behavioural transitions (i.e., the likelihood of one following another in a sequence) and calculating spontaneous alternation behaviour (SAB) scores (i.e., the ratio of actual behaviours observed to the possible number of behaviours that are possible in a sequence, following Jones *et al*., 2011).

I made four predictions: 1) With increasing complexity of the puzzle boxes, the mongooses would take longer to obtain the food incentive (increased latency to consume from stage 1 to stage 4) and perform a greater frequency of specific behaviours such as investigating, digging and vigilance etc, because the mongooses would need to engage with the device for longer as the complexity increased. 2) There would be a greater number of significant behavioural transitions and higher SAB scores as the complexity of the devices increased, since the mongooses need to make different decisions about how to access the food incentive with increasing complexity. 3) Due to differences in their habituation to people and prior regular engagement with anthropogenic food in various devices (e.g., bins), I expected that less urbanised animals would be better decision makers (i.e., be better problem-solvers) and have fewer behavioural transitions and reduced SAB scores (enhancing their decision making abilities) because they would be less disturbed by anthropogenic factors such as human presence, noise and pollution compared to more urbanised areas. 4) The latency to consume, frequency of behaviours, behavioural transitions and SAB scores would differ between two areas with different levels of human disturbance.

Material and methods

Study site

The study was conducted in two locations, the Meyersdal Nature Estate (26°18'08.2"S 28°04'55.9"E) and the Meyersdal Eco Estate (26°17'03.6"S 28°04'50.8"E) in the larger 1080 ha Meyersdal nature area. The estate is located within the south of Johannesburg, Gauteng, South Africa (Figure 1). The climate in the Meyersdal area is warm and temperate with average annual temperatures around 16°C. The area receives summer rainfall with average precipitation of approximately 755 mm per year.

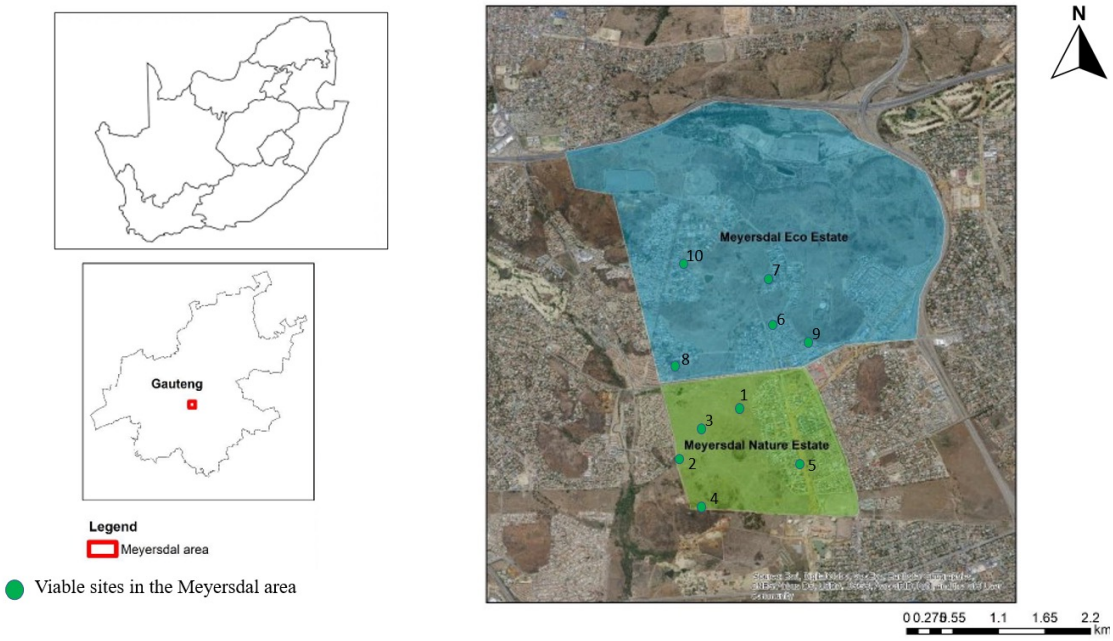


Figure 1. Map of the Meyersdal nature area with yellow mongoose den sites used in the study. An insert of South Africa and Gauteng is provided for reference.

The Nature Estate was 300 ha in size, although at the time of my study only 15% of the area had been developed for human housing, while the rest of the area remained untouched. The nature area in the Nature Estate, where the wildlife normally occurs, is fenced off from the residential area with palisade fencing and, in some areas, with electric fencing (pers. obs.). The nature area is accessible to the residents, hikers, pedestrians and occasionally cyclists. The Eco Estate was 480 ha in size, located directly north of the Nature Estate. The wildlife here is not fenced off from the houses in the Eco Estate and are free to roam and travel between houses. Therefore, animals in the Eco Estate often encounter humans; and smaller animals such as small carnivores, frequently enter the gardens of human

residents. Yellow mongoose colonies have been recorded near the human residential areas (pers. obs). The level of human-animal interaction differs between the two locations, since the wildlife is fenced off from the human residences in the Nature Estate and animals encounter humans less often compared to in the Eco Estate.

The natural areas in both the Nature Estate and the Eco Estate are largely dominated by indigenous plants and grassland, and largely abundant in thatch grass (*Hyparrhenia hirta*) and red grass (*Themeda triandra*; Cronk and Pillay, 2019). Small herbivores such as scrub hares (*Lepus saxatilis*) and meso-carnivores such as yellow mongooses (*Cynictis penicillata*) and slender mongooses (*Galerella sanguinea*) occur in both estates and their colonies are widespread throughout the two locations. Other mammalian species occur throughout both reserves, such as zebra (*Equus burchelli*), blue wildebeest (*Connochaetes gnou),* rock hyrax (*Procavia capensis*), eland (*Taurotragus oryx*) and kudu (*Tragelaphus strepsiceros*), and various bird species and numerous species of small lizards (pers. obs.) are found in the area.

Experimental design and protocol

In 2019, 10 sites (five in the Nature Estate and five in the Eco Estate) were selected for study with an average distance of 12 ha between each site (average home range of urban yellow mongooses; Cronk and Pillay, 2019). Sites in both estates were selected based on frequency of sightings or presence of dens of the yellow mongooses; not all dens were found. Yellow mongooses were unlikely to cross over between estates due to the freeway between the estates and a previous study found only one mongoose was able to cross over (Cronk and Pillay, 2018). The sites were selected by putting out meat and monitoring whether a yellow mongoose appeared. If a mongoose came to eat the meat, then that was considered a viable site and considered for experiments. Data were collected from March 2019 to September 2019.

Puzzle box design

Problem-solving in urban yellow mongooses was tested using puzzle boxes containing a food incentive. The rectangular puzzle boxes were constructed of clear Perspex, with two metal hinges which allowed the lid to be opened and closed. The boxes were 70 mm in height, 230 mm in length, and 150 mm in breath (Figure 2). The puzzle boxes were placed where yellow mongooses were frequently sighted. This was done to allow the mongoose to habituate to the puzzle box (novel object). Deli meat offcuts (1 teaspoon) were placed in the box on the side the lid to attract the mongoose and served as an incentive to solve the puzzle.

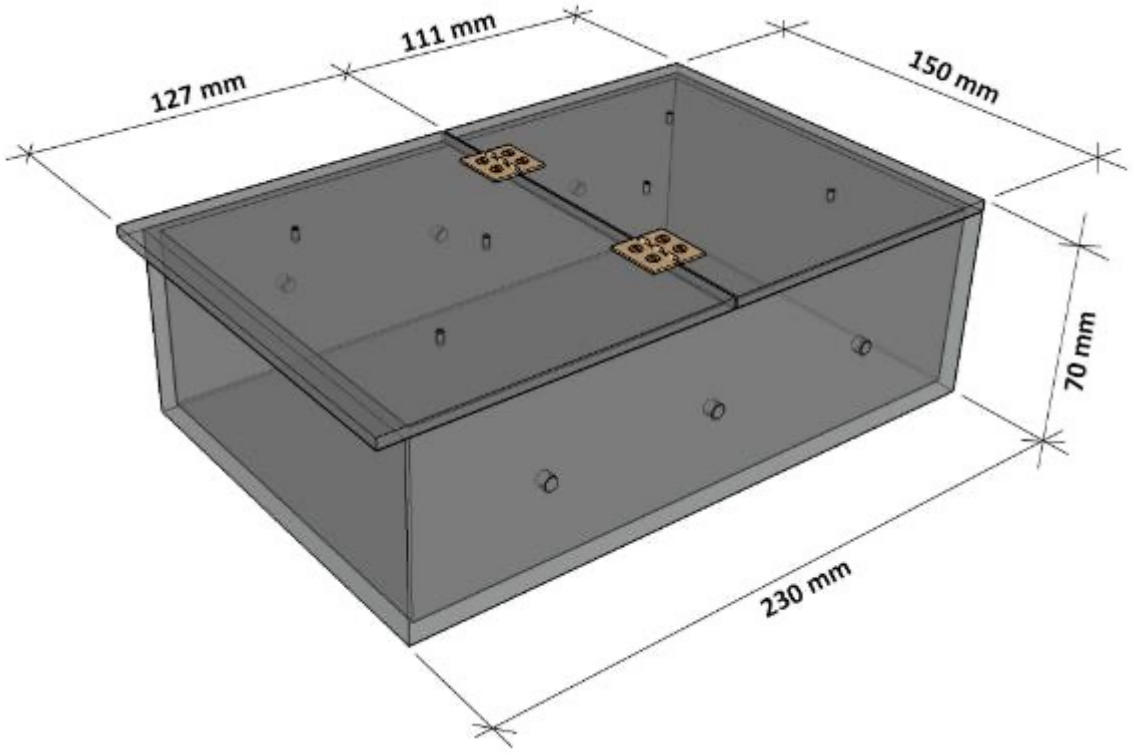


Figure 2. A diagram of the Perspex box used to test the problem-solving abilities of yellow mongoose. The small holes around the box allowed for the mongooses to smell the food incentive inside the box and the clear Perspex allowed the animal to see the food incentive (diagram by M. Muller).

Experimental procedure

I used a puzzle box that increased in complexity to open and access the food incentive to test the problem-solving abilities of the yellow mongooses. The experiment consisted of four successive stages of complexity:

- Stage 1: the open box stage. The lid of the puzzle box was completely open, allowing the mongoose to access the food directly (Figure 3a). Stage 1 allowed the mongoose to habituate to the puzzle box, so that the mongoose did not perceive the box as a threat and the food was used as a positive reinforcement.
- Stage 2: the propped lid stage. The lid of the puzzle box was propped up with a stick, that allowed the box lid to open approximately 10 mm, seen in (Figure 3b). This enabled the mongoose to access the food by using their snouts to open the box.

- Stage 3: the closed lid stage. The lid of the puzzle box was completely closed (Figure 3c). The mongoose was required to locate the position of the lid and then flip the lid open to access the food incentive.
- Stage 4: the impediment stage. A 200 g (approximately 20% of the average body weight of a yellow mongoose) impediment made of gravel wrapped in a piece of hessian sack was placed on top of the lid and tied to the bottom to secure it to the puzzle box (Figure 3d). In this stage, the mongooses were required to first remove the impediment from the lid before being able to lift the lid and access the food incentive.

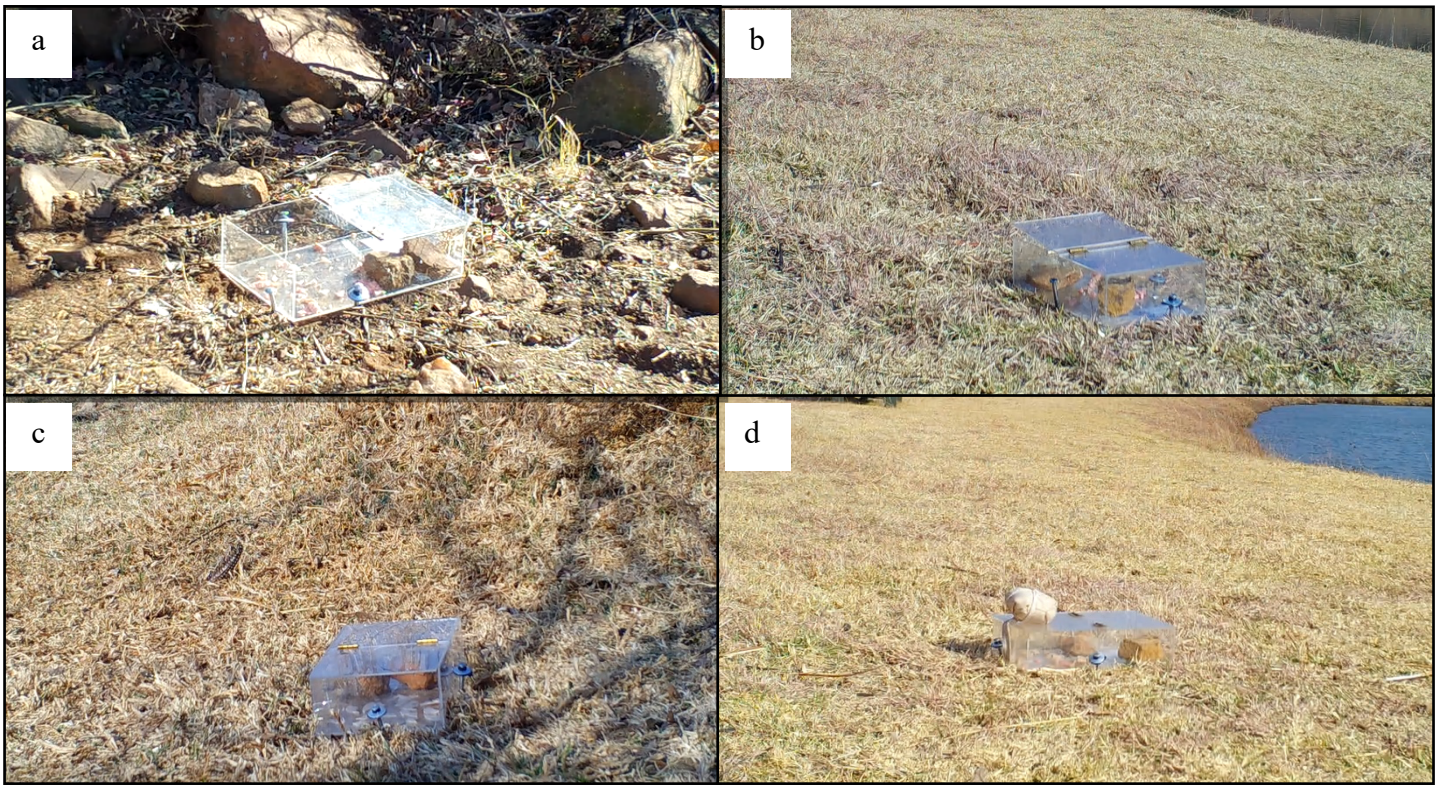


Figure 3. Photographs of the stages in the puzzle box experiment. (a) Stage 1, the puzzle box completely open; (b) Stage 2, the puzzle box lid propped open with a stick; (c) Stage 3, puzzle box completely closed; and (d) Stage 4, puzzle box completely closed with an impediment on the lid.

Four stages (with 10 trials per stage) were tested across three pilot trial sites that formed part of the experimental design, and a cumulative frequency graph was constructed to establish the specific number of trials in each stage the mongooses required to successfully reach the solution. The optimal number of trials was established based on where the graph plateaued. Once the mongoose learnt the skill, I moved on to the next stage. The cumulative

frequency curve indicated the number of trials needed for each stage was: five trials for stage 1, five trials for stage 2, six trials for stage 3 and nine trials for stage 4. Stages 1 and 2 were set out for 120 hours, stage 3 was set out for 144 hours and stage 4 for 216 hours.

I used Bushnell Essential trophy camera traps that are trigged by motion sensors to remotely record the behaviours of the mongooses and their interactions with the puzzle box. The camera trap was either tied to a tree or set up on a tripod approximately 1-2 metres away from the puzzle box with an approximate 42.3° viewing angle, ensuring that the entire puzzle box was within view of the camera. The distance between the camera trap and the puzzle box for each site was kept constant throughout the experiment. Using camera traps allowed me to obtain video recordings of the mongooses without disturbing them unnecessarily.

I set up the puzzle box as close to the den as possible to ensure other mongooses did not interfere with the experiment. I considered a trial as being each time the puzzle box was set out with a food incentive A trial began when a mongoose first appeared in a camera's field of view until it contacted the food incentive inside the puzzle box or if the mongoose approached the box and left which terminated a trial. The puzzle box experiments were set up on consecutive mornings between 8 am to 11 am but the boxes were left permanently in the field to ensure the mongoose remained habituated to the puzzle box. Before the start of the trial, I replenished the food incentive with fresh meat, changed the batteries of the camera trap, and rotated the puzzle box randomly at approximately 45°. Rotating the puzzle box at each trial ensured that the mongooses did not become habituated to the lid being at a particular orientation of the box. The puzzle box was secured by placing small rocks inside the box and knocking four nails into the ground on the outside of each side of the puzzle box to hold the box in place. By securing the box in this way, I ensured the mongooses did not move the box out of view of the camera trap. As soon as a trial was set up, I left the site. Management of the Meyersdal Estates did not provide permission for the trapping and marking of individuals for identification, but individuals could be reliably identified using body morphology, idiosyncratic markings and behaviour. In all cases, the same mongoose accessed the puzzle box. Yellow mongooses are sexually monomorphic in body size and general appearance, and therefore the sex of the mongoose engaging with the device could not be established from camera trap footage.

Latency to consume the food incentive and behaviours

From camera trap footage, I obtained latency to consume measured in seconds and the frequency of behaviours are observed from the time the mongoose made contact with the

puzzle box until it retrieved the food incentive. The latency (in seconds) to consume the food incentive was measured from the moment the mongoose contacted the puzzle box until it obtained the food incentive. The behaviours that were frequently displayed by the mongooses were recorded (Table 1).

Table 1. Definitions of the behaviours recorded in the puzzle box experiment.

Behaviour		Description
Investigating	Sniffing	Nose contacting the box without biting or moving the box.
	Biting	Touching any part of the box with the mouth; clamping down on the box with teeth.
	Pawing	Scratching the lid of the box with paws.
	Locomotion	Circling the puzzle box.
	Pulling	Moving the box towards the body using any body part.
	Pushing	Moving the box away from the body using any body part.
Digging		Displacing ground/grass at the base of the box with forepaws.
Vigilance		Observing the environment by propping the head up and looking around, staring into the distance, may also stand on the hind legs.

Frequency of behaviours

The frequency of behaviours was recorded as the number of times each behaviour occurred from the time a mongoose contacted the box until the time the food incentive was obtained to provide an overall count of the behaviours displayed by the mongoose. The behaviours were categorised as follows to account for low frequency (zero value of certain behaviours) of occurrence for each behaviour: (i) investigating (included sniffing, locomotion, biting, pawing, pulling, pushing), (ii) digging around the box (scored separately since this behaviour did not involve the mongoose directly interacting with the puzzle box) and (iii) vigilance (Table 1). To account for the different interaction times (varying latency to consume times) in each trial, the frequency of each behaviour in each trial was divided by the

total time taken to complete the trial (frequency of X/total time of the trial). The frequency per trial was summed as a total for each stage of complexity within each of the two locations.

Behavioural transitions

I used behavioural transitional matrices to analyse the likelihood of one behaviour following another while the mongooses were interacting with the puzzle box. Behavioural transitions show the overall pattern of behaviours during the problem solving at each stage. To analyse behavioural transitions, I constructed transition matrices. A transition matrix is a square table of behavioural elements in which the total number of times each behaviour is followed by another is recorded. Since any behavioural pattern cannot be followed by itself, diagonal cells were structural zeros (left blank). To use transitional matrices to analyse behavioural patterns, I had to ensure that the correlations among the behavioural patterns was stable (Spruijt and Gispen, 1984). For correlations to be assessed as stable, the following requirements need to be met: (1) the minimum number of transitions has to be more than five times the behavioural patterns (Spruijt and Gispen, 1984); (2) in the overall matrix, at least 80% of the cells have to be filled (Casarrubea *et al*., 2008); and (3) the number of subjects has to be more than the number of variables (for both the columns and rows, Short and Horn, 1984). According to Spruijt and Gispen (1984), poorly filled matrices could present a serious issue in multivariate analyses. Therefore, all the trials (across stages and sites) were combined into one matrix to generate stable transitional matrices. The matrices were then analysed using MatMan (version 1, Noldus Information Technology, Netherlands) a software for matrix analysis and manipulation. The matrices were first normalized using the matrix normalization function on MatMan and then adjusted residuals were obtained. Adjusted residuals are values representing the difference between the observed and the expected values. Positive values indicate transitions occurring more often than expected and negative values indicate values occurring less often than expected by chance. The values obtained from the adjusted residual matrices were expressed according to the Z-distribution at $\alpha = 0.05$. The adjusted residual matrices were then represented in path diagrams with arrows indicating the level of association between behaviours. I summed matrices as sites 1-5 (Nature Estate) and sites 6-10 (Eco Estate) using MatMan, and plotted path diagrams (kinetograms) showing only statistically significant transitions for each stage to compare the number of significant transitions per stage at each location. The thickness of the arrows is

proportional to the likelihood of occurrence of each behavioural transition. Stage 1 was excluded from this process as there were no significant transitions observed for this stage.

Matrix correlation

To analyse whether there were similarities in the transitions between the stages and between sites, I compared the matrices using matrix correlation in MatMan. All the trials were summed up per stage per location/site (see above). I compared matrices between each stage as per location. The matrices were calculated using Mantel's Z and Pearson's r tests. The significance of the correlations was set to 2000 permutations to assess the deviation between the Mantel's Z-value and the actual Z-values.

Spontaneous alternation behaviour score

Spontaneous alternation behaviour (SAB) explains a subject's tendency to alternate consecutive, nonreinforced directional behaviours while exploring (Hughes, 2004). SAB analyses have been used to show whether animals are more perseverative in their behaviours (i.e., repeat the same behaviours without a change in the outcome; Rothacher *et al*., 2020). SAB scores were calculated as the ratio of actual behaviours observed to the number of behaviours that are possible in a sequence, following Jones *et al*. (2011). A total of eight different behaviours (sniffing, biting, pawing, locomotion, pulling, pushing, digging and vigilance) were observed (Table 1) while the mongooses were interacting with the puzzle box. For example, in the behavioural sequence sniff, locomotion, vigilance, dig, sniff, vigilance, dig, sniff the mongoose exhibited four different behaviours out of a possible eight total behaviours, then the SAB score would be 4/8= 0.5 for the first sequence of 8 behaviours. I then shifted the frame one place up to the next eight, starting with locomotion, then vigilance, etc. The average SAB scores per trial were summed for each stage at both locations. Stage 1; open box stage, the food was easily accessible and therefore a very low frequency of behaviours was recorded. In most cases the mongoose would sniff the box and consume the food incentive (end of trail). Therefore stage 1 was excluded from this calculation because the mongooses performed on average fewer than 8 behaviours per trial at most sites.

Statistical analyses

An ethogram of the most frequent behaviours observed was constructed. Analyses for the latency of completing the task and frequency of behaviours were performed with R

Statistical Software (R version 3.4.3; R Core Team, 2017). Shapiro-Wilk tests were used to test for normality. Non-normal data were transformed using Box-Cox transformations (R package: MASS); for variables that could not be transformed, non-parametric tests were used. The significant level was set at 0.05. A linear mixed-effects model (R packages: lme4, lmerTest) was used to analyse the time taken to complete the task (family = Gaussian; link = log). The frequency of behaviours was analysed using generalized mixed-effects models that were constructed using the glmmPQL function in the *lme4* package (family = poisson; link = log) and all statistical tests were performed using the Anova function in the *car* package. Stage was included as the repeated measures variable, with stage and location as fixed factors and site and trial as random factors. Post hoc tests to determine the pairwise differences for the significant fixed factors were performed using Tukey post hoc tests (R package: multcomp).

Behavioural matrices and the matrix correlations were analysed using MatMan, a program used for matrix analysis and manipulation, as described above.

Statistical analyses for SAB scores were performed with R Statistical Software (R version 3.4.3; R Core Team, 2017). The data were non-normal (Shapiro-Wilk test) and therefore non-parametric tests were used. The significant level was set at 0.05. Generalized mixed models were constructed using the function glmmPQL in the *lme4* package (family = poisson; link = log) and all statistical tests were performed using the Anova function in the *car* package. The various stages were a fixed repeated measures variable, with stage and location as fixed factors and site and trial as random factors. Tukey post hoc test were performed to determine the pairwise differences for the significant fixed factors (R package: multcomp).

Results

Behaviours were analysed from camera trap footage taken between March to September 2019 in 10 sites (5 sites in the Nature Estate and 5 in the Eco Estate). The mongooses (N=10) were successful in obtaining the food incentive in all trials (i.e., 100% success).

Table 2: The number of trials per puzzle box set up at each stage of complexity.

Stage	1	2	3	4
Number of trials	5	5	6	9

Latency of completing the task

Location ($\chi^2 = 10.26$, df = 1, $p < 0.001$) and stage ($\chi^2 = 145$, df= 3, $p< 0.001$) were significant predictors of the time taken to complete the task (Figure 4a). The latency to obtain the food incentive was significantly longer in the Eco Estate compared to the Nature Estate (Figure 4a). The mongooses took significantly longer to obtain the food incentive in stage 4 and were quickest in stage 1; there was overlap between stages 2 and 3, which occupied an intermediate position between stages 1 and 4 (Figure 4b). On average, it took the mongooses 10 seconds to obtain the food incentive in stage 1 and 72 seconds in stage 4 across the 10 sites. The stage*location interaction ($\chi^2 = 0.884$, df= 3, $p = 0.829$) was not a significant predictor of the latency of completing the task.

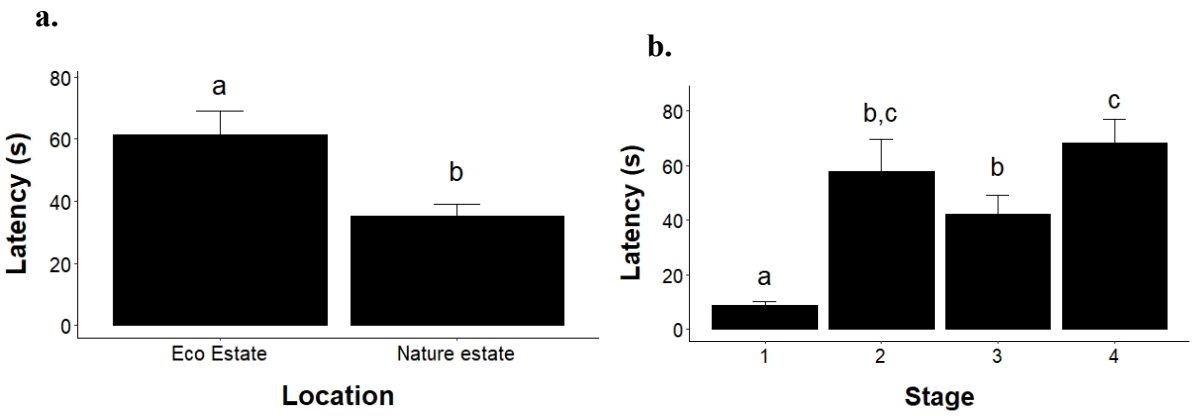


Figure 4**.** The Mean±SE latency to complete the puzzle box task (a) by location, and (b) by stage. Letters denote significant differences, with non-significant differences between groups indicated with the same letter.

Frequency of behaviours

The behaviours that occurred from the time the mongoose approached the puzzle box until the time the mongoose consumed the food incentive were summed and analysed.

Digging

Stage was a significant predictor of how often the yellow mongooses dug under or close to the puzzle box (Table 3). Post hoc results showed that the frequency of digging was significantly lower in stage 1 compared to the subsequent stages; stages 2, 3 and 4 did not differ statistically (Table 3; Figure 5). Location and the stage*location interaction were not significant predictors of the frequency of digging (Table 1).

Table 3. General linear mixed-effects model statistical output for the frequency of digging, investigating and vigilance by yellow mongooses in four stages of complexity across two locations (N=10). Significant effects are in bold.

Factors	χ^2	**Degrees of freedom**	p-**value**
Digging			
Location	0.00	1	1.000
Stage	**18**	**3**	**<0.001**
Location*Stage	5	3	0.172
Investigating			
Location	**3.97**	**1**	**<0.001**
Stage	**16.47**	**3**	**0.050**
Location*Stage	0.86	3	0.676
Vigilance			
Location	**5.5**	**1**	**<0.001**
Stage	**25.21**	**3**	**0.050**
Location*Stage	6.63	3	0.085

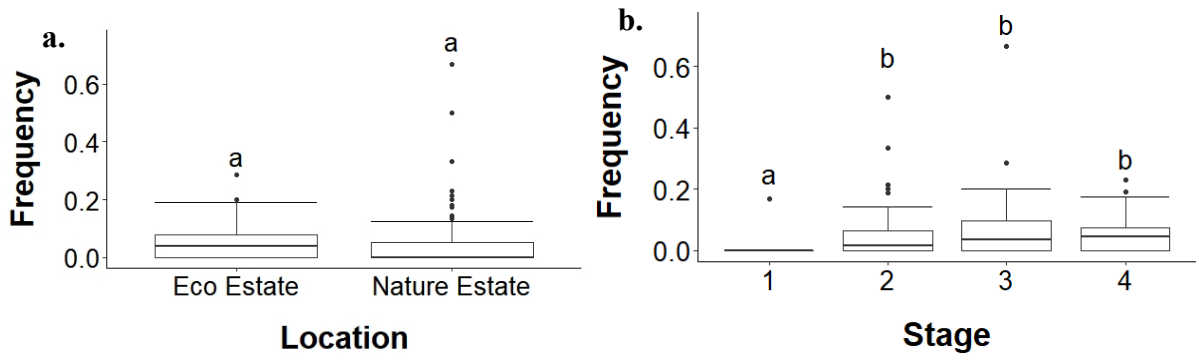


Figure 5. The frequency of digging when the yellow mongooses were interacting with the puzzle box (a) across locations and (b) four stages of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, the error bars indicate 95% confidence intervals and the dots above the error bar indicate outliers. The same denotes stages that are not significantly different.

Investigating

Location and stage were significant predictors of how frequently the yellow mongooses investigated the puzzle box (Table 3). Post hoc tests for location showed that the mongooses investigated the puzzle boxes more frequently in the Eco Estate compared to the Nature Estate (Figure 6a). Mongooses also investigated the puzzle box significantly more frequently in stage 1 compared to the other stages (Figure 6b). The interaction between stage and location was not a significant predictor of the frequency of investigating.

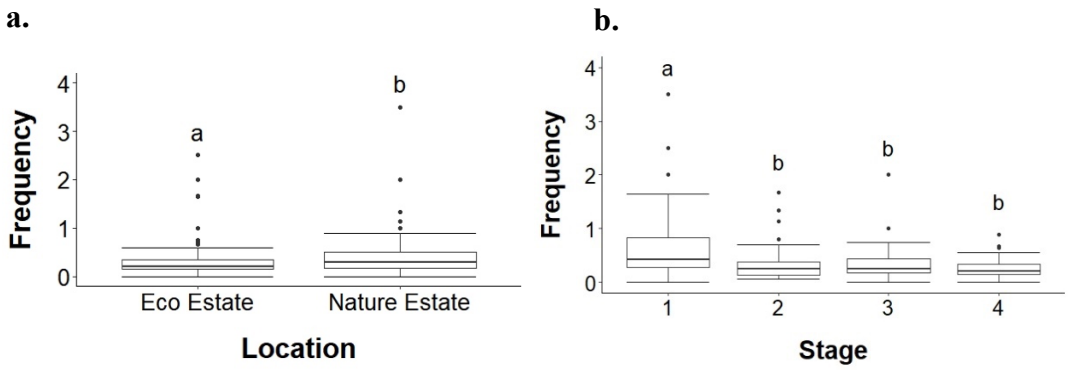


Figure 6. The frequency of investigating when the mongooses were interacting the puzzle box (a) across locations and (b) at four stages of complexity. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, the error bars indicate 95% confidence intervals and the dots above the error bar indicate outliers. Letters denote significant differences, with non-significant differences between groups indicated with the same letter.

Vigilance

Stage and location were significant predictors of how frequently the mongooses became vigilant. The stage*location interaction was not a significant predictor of vigilance (Table 3). Post hoc tests showed that the frequency of vigilance was higher in the Eco Estate than in the Nature Estate (Figure 7a). Across stages, mongooses were more vigilant in stage 1 and the least vigilant in stage 4 (Figure 7b).

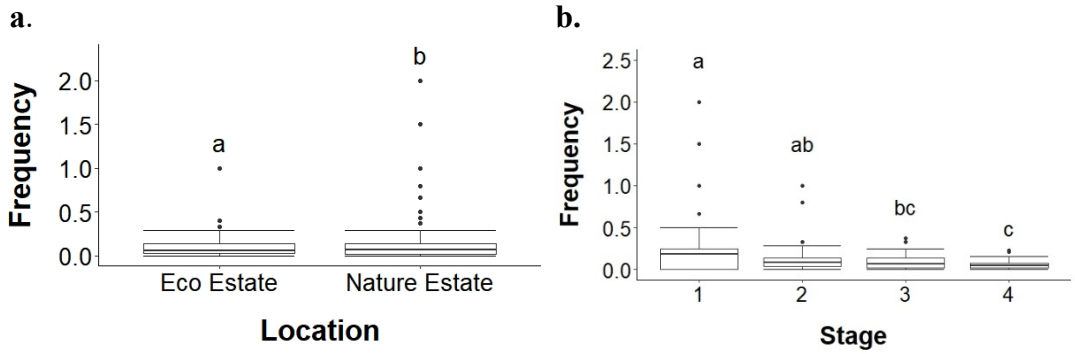


Figure 7. The frequency of vigilance between (a) locations and (b) stages. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, the error bars 95% indicate confidence intervals and the dots above the error bar indicate outliers. Letters denote significant differences, with non-significant differences between groups indicated with the same letter.

Behavioural transitions (transitional matrices)

No significant transition was recorded in stage 1 at any of the locations. Therefore, the transitions for this stage were excluded from this section. The number of significant transitions increased as the complexity of the stages increased, except for stage 3 in the Nature Estate where there were only two significant behavioural transitions.

For stage 2 in the Nature Estate, five behavioural transitions were significantly different from what would be expected by chance (Figure 8a). The transitions from pawing to vigilance, and from digging to vigilance occurred more often than chance. In contrast, the transitions from digging to sniffing, and from locomotion to pawing occurred less often than chance (Figure 8a). In the Eco Estate (Figure 8b), the mongooses were more likely to transition from sniffing to locomotion, and from sniffing to pawing, but were less likely to transition from sniffing to vigilance. The mongooses transitioned from digging to vigilance, and from digging to biting. The mongooses transitioned from biting to pawing, and from pawing to biting. There were more significant behavioural transitions in the Eco Estate compared to the Nature Estate in stage 2.

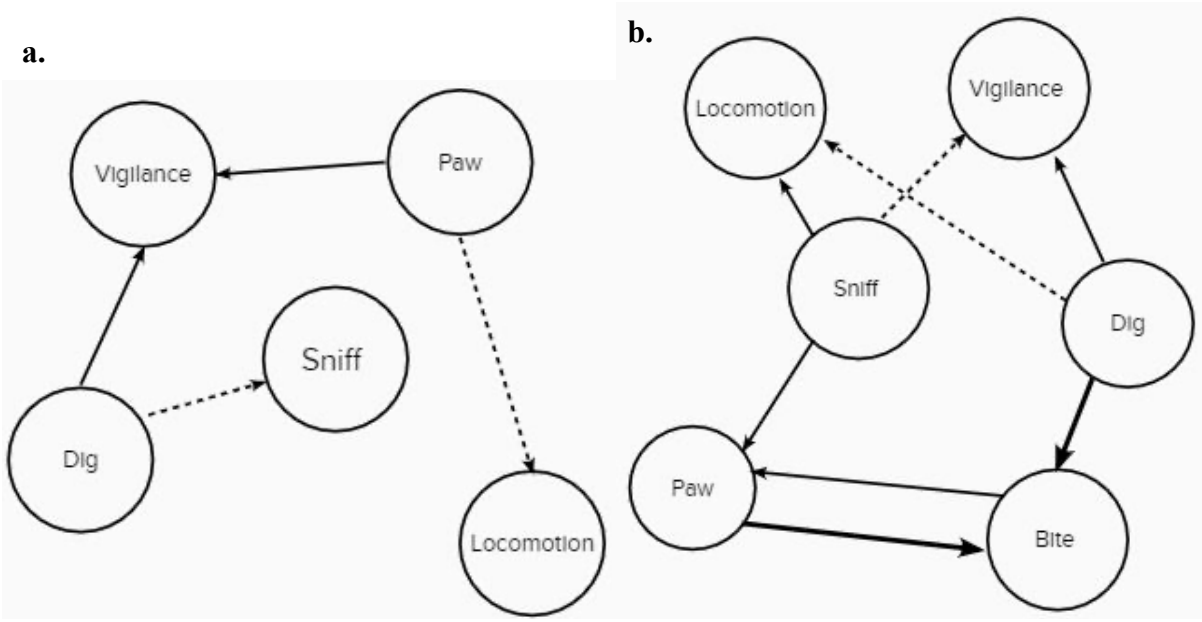


Figure 8. Behavioural kinetograms of yellow mongoose behavioural transitions in Stage 2 in (a) the Nature Estate, and (b) the Eco Estate. Only behaviours that showed significant transitions are shown. The thickness of the arrows is proportional to the likelihood of occurrence of each behavioural transition. Solid lines show transitions occurring more than chance and dotted lines show transitions occurring less often than chance. Thin arrows show $Z > 1.96$, thin dashed arrows show $Z < -1.96$, medium arrows show $Z > 2.58$.

For stage 2 in the Eco Estate, six behavioural transitions were significantly different from what would be expected by chance. The transitions from sniffing to pawing, sniffing to locomotion, pawing to biting, biting to pawing, digging to biting and biting to vigilance occurred more likely than chance. The transition from digging to locomotion, and from sniffing to vigilance occurred less frequently than chance.

For stage 3 in the Nature Estate, there were significant bidirectional transitions between two behaviours and the relationship between pawing and digging, which occurred more than chance (Figure 9a). In the Eco Estate, five behavioural transitions were significantly different from what would be expected by chance (Figure 9b): the transitions from digging to vigilance, pawing to vigilance, locomotion to sniffing, and sniffing to locomotion occurred significantly more frequently than chance. The transitions from digging to locomotion, digging to pawing, vigilance to sniffing, locomotion to vigilance, and locomotion to digging occurred significantly less frequently than chance.

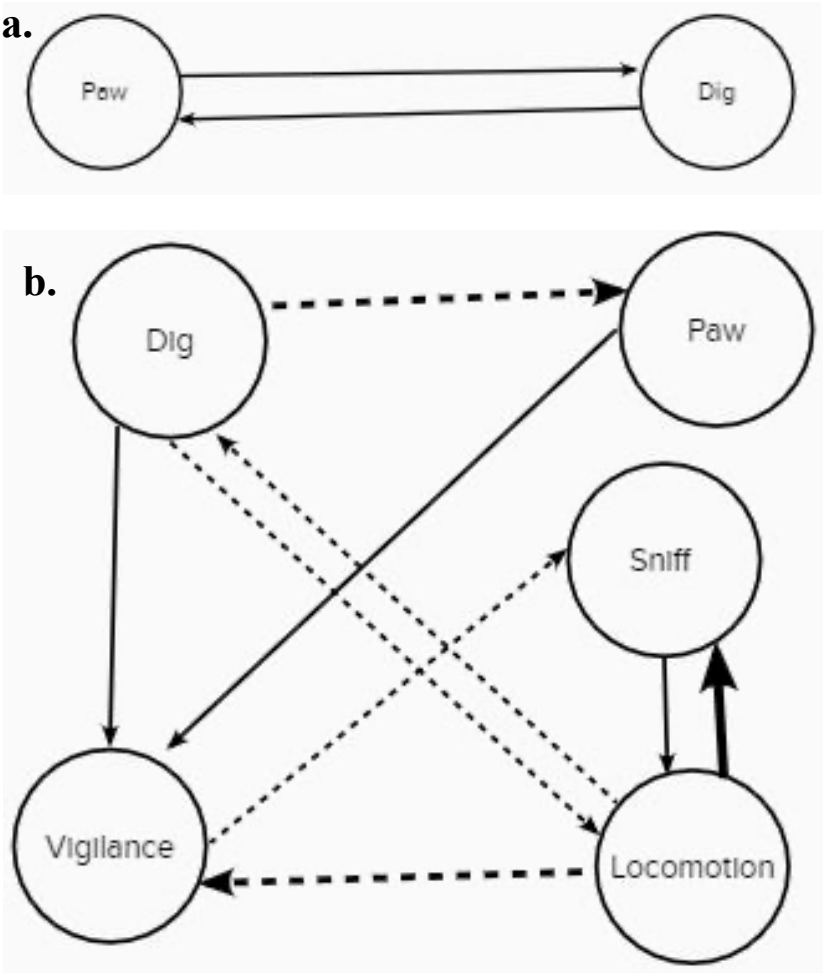


Figure 9. Behavioural kinetograms of Stage 3 in (a) the Nature Estate and (b) the Eco Estate. Only the behaviours that showed transitions significantly different from chance are shown. The thickness of the arrows is proportional to the likelihood of occurrence of each behavioural transition. Solid lines indicate transitions occurring more than chance, and dotted lines indicate transitions occurring less frequently than chance. Thin arrows indicate Z >1.96, thin dashed arrows show Z < -1.96, medium arrows show Z >2.58, medium dashed arrows show Z< -2.58 thick arrows, Z >3.29.

For stage 4 in the Nature Estate, there were significant transitions between all eight behaviours (Figure 10a). The transitions from locomotion to sniffing, pawing to pulling, pawing to digging, pulling to digging, biting to digging, digging to vigilance, pushing to locomotion and sniffing to locomotion occurred significantly more than chance. The transition from locomotion to vigilance, locomotion to pawing, pawing to locomotion (bidirectional), pawing to vigilance, sniffing to vigilance, digging to sniff, pushing to sniffing

and pushing to vigilance occurred significantly less likely than chance. In the Eco Estate, there was significant transitions between seven behaviours (Figure 10b). The transition from locomotion to sniffing, sniffing to locomotion (bidirectional), sniffing to biting, digging to vigilance, pawing to vigilance, sniffing to pushing, and pushing to vigilance occurred significantly more likely than chance. The transition from sniffing to vigilance and digging to sniffing occurred significantly less likely than chance.

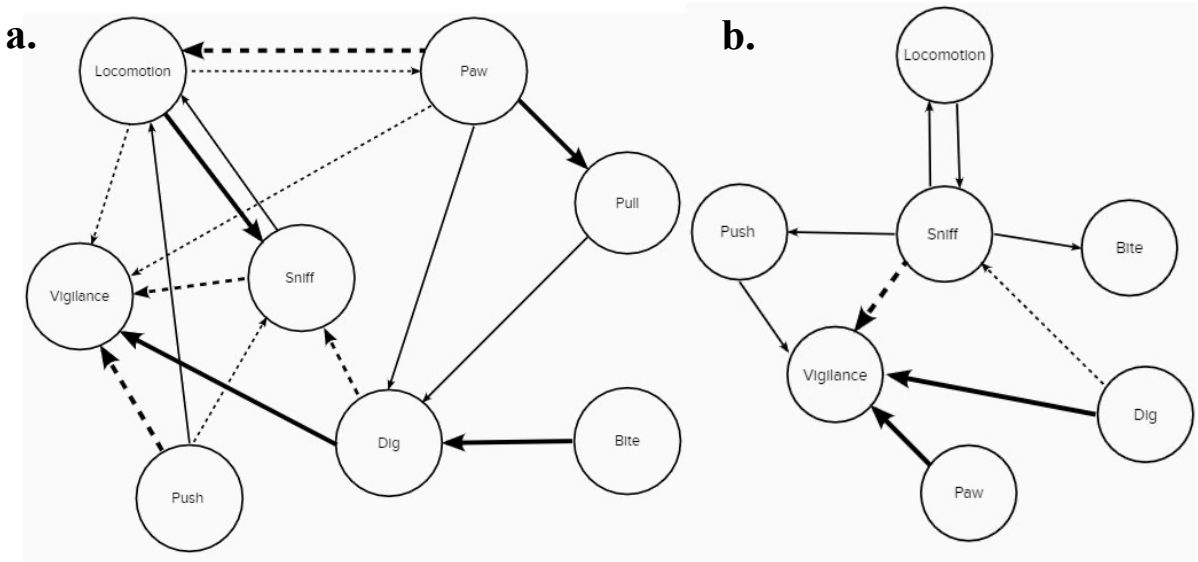


Figure 10. Behavioural kinetograms of stage 4 in (a) the Nature Estate, and (b) Eco Estate. Only the behaviours that showed significant transitions are indicated. The thickness of the arrows is proportional to the likelihood of occurrence of each behavioural transition. Solid lines show transitions occurring more than chance and dotted lines show transitions occurring less often than chance. Thin arrows show Z >1.96, thin dashed arrows show Z < -1.96, medium arrows show Z >2.58, medium dashed arrows show Z< -2.58 thick arrows, Z >3.29 thick dashed arrows show Z < -3.29.

Matrix correlations

To analyse whether there were similarities in the behavioural transitions between the stages and between sites in each location, I compared the behavioural transitional matrices. I analysed matrices between each stage per location/sites. I compared the transitional matrices of each stage in combination: stage 2 compared to stage 3, stage 2 compared to stage 4, and stage 3 compared to stage 4 in the Nature Estate and in the Eco Estate (Table 4). I found that

73% of the overall correlations were significant. Comparison between stage 2 and stage 3 was significant in the two locations. The overall matrices (sites summed for Nature Estate and Eco Estate) indicated that the behavioural transitions were significantly correlated (Table 5).

Table 4. Pairwise correlation of behavioural transitional matrices in between stages per location/site. Highlighted cells indicate a significant relationship ($p < 0.050$) and r^2 values that are highly correlated ($r^2 > 0.600$) are shown in bold.

Location/Site	Stage 2 vs Stage 3	Stage 2 vs Stage 4	Stage 3 vs Stage 4
Nature Estate 1	**$r^2 = 0.780$** p = 0.011	**$r^2 = 0.823$** p = 0.003	**$r^2 = 0.672$** p = 0.017
Nature Estate 2	**$r^2 = 0.721$** p = 0.004	**$r^2 = 0.687$** p = 0.002	$r^2 = 0.591$ p = 0.015
Nature Estate 3	**$r^2 = 0.944$** p = 0.001	$r^2 = 0.488$ p = 0.043	$r^2 = 0.386$ p = 0.062
Nature Estate 4	**$r^2 = 0.676$** p = 0.012	$r^2 = 0.348$ p = 0.041	$r^2 = 0.454$ p = 0.010
Nature Estate 5	**$r^2 = 0.681$** p = 0.002	$r^2 = 0.194$ p = 0.132	$r^2 = 0.235$ p = 0.102
Eco Estate 1	**$r^2 = 0.586$** p = 0.003	$r^2 = 0.530$ p = 0.019	$r^2 = 0.543$ p = 0.002
Eco Estate 2	**$r^2 = 0.675$** p = 0.001	**$r^2 = 0.789$** p = 0.001	$r^2 = 0.507$ p = 0.012
Eco Estate 3	**$r^2 = 0.749$** p = 0.001	$r^2 = 0.451$ p = 0.022	$r^2 = 0.283$ p = 0.080

Eco Estate 4	**$r^2 = 0.702$** p = 0.001	**$r^2 = 0.589$** p = 0.012	**$r^2 = 0.689$** p = 0.006
Eco Estate 5	**$r^2 = 0.566$** p = 0.003	$r^2 = 0.356$ p = 0.051	**$r^2 = 0.559$** p = 0.003

Table 5. Pairwise correlation of behavioural transitional matrices of yellow mongoose between the locations for each stage. Cells that are highlighted show a significant relationship between variables ($p<0.05$) and r^2 values that indicate variables are highly correlated ($r^2>0.6$) are shown in bold.

Location	Stage 2	Stage 3	Stage 4
Nature Estate Vs Eco Estate	**$r^2 = 0.869$** p = 0.003	**$r^2 = 0.819$** p = 0.002	**$r^2 = 0.911$** p = 0.001

Spontaneous alternation behaviour (SAB) Scores

Location and stage were significant predictors of the SAB score (Table 7). The higher SAB score in the Nature Estate compared to the Eco Estate (Figure 11a) indicates that the mongooses were alternating between more behaviours in the Nature Estate than the Eco Estate. The SAB score was also significantly different between stage 3 and stage 4 but there was no significant difference between stage 2 and 3 (Figure 11b).

Table 7. General linear mixed-effects model statistical output on the SAB score while the mongooses were interacting with the puzzle box over three stages of complexity across two locations (N=10). Significant effects are indicated in bold.

Variable	χ^2	Degrees of freedom	p-value
Location	**7.33**	**1**	**< 0.001**
Stage	**7.50**	**2**	**0.050**
Location*Stage	4.35	2	0.114

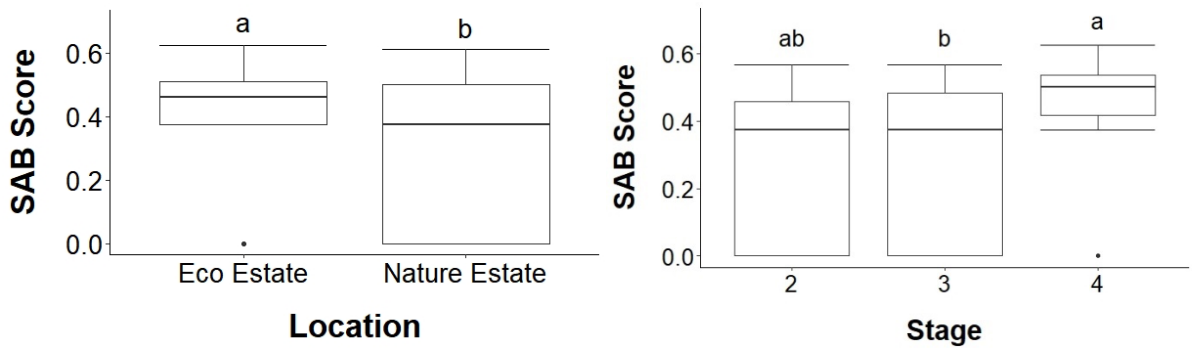


Figure 11. The SAB scores generated from the yellow mongooses were interacting the puzzle box in (a) the Nature Estate and the Eco Estate, and (b) across stages. The boxes indicate the upper and lower quartiles, the horizontal lines indicate medians, the error bars indicate 95% confidence intervals and the dots above the error bars indicate outliers. The same alphabet denotes stages that are not significantly different.

Discussion

The aim of my study was to assess decision-making during problem-solving and innovation in an urban dwelling population of yellow mongooses (*Cynictis penicillata*). I used a puzzle box task to assess whether the yellow mongooses could learn to access a food incentive. The puzzle box task increased in complexity sequentially from an open box (stage 1), propped lid (stage 2), closed lid (stage 3) and an impediment (stage 4). The puzzle boxes were set up close to yellow mongoose colonies in two separated areas in an urban estate with differing levels of anthropogenic disturbance.

My first prediction was that with increasing complexity of the puzzle box task, the latency to consume the food incentive would increase. The latency to consume the food increased from stage 1 to stage 2 but there was no significant difference in the latency between stages 2 and 3 or between stages 2 and 4. The similarity in latency between these stages is likely due to the mongoose learning the basic skill of "how to flip the lid" and were then able to apply this skill in subsequent stages.

To engage with a novel situation/object, like the novel puzzle box, an individual must not regard it as a threat and be willing to engage with the novel object. As a result, neophobia (if it exists) must be overcome because it might hamper problem-solving abilities (Webster and Lefebvre, 2001; Greenberg, 2003; Auersperg *et al.,* 2011), as evidenced by the development of innovative behaviour in birds. Problem-solving and innovation studied in common myans (*Sturnus tristis*) showed that increased neophobia may reduce an individual's likelihood of approaching a novel object and therefore reducing its problem- solving abilities (Sol *et al*., 2012). Huebner and Fichtel (2015) therefore noted that familiarity with a novel object reduces the effects of neophobia. The open box stage (stage 1) was therefore used to allow for habituation of the yellow mongooses to the novel object to obtain the food incentive, ensuring that they learnt that interacting with the puzzle box provided a food reward. Yet, a study in callitrichid monkeys (Callitrichidae) found that overcoming habituation alone was not enough for the development of problem-solving abilities (Kendal *et al.*, 2005). Factors such as behavioural flexibility and persistence in finding a solution to a problem, may also be critical for learning (Griffin and Guez, 2014). For example, problem-solving and innovation studies in spotted hyenas (*Crocuta crocuta*) found that individuals that were more persistent in engaging with a novel object were more likely to solve the problem compared to those that gave up shortly after being exposed to the problem (Benson-Amram and Holekamp, 2012; Benson-Amram *et al.*, 2013). Yet, individuals that are

persistent in their behaviours that prove ineffective in solving a problem and that are not able to modify their behaviours to find a new solution may be less likely to find solutions (Hauser, 1999). Similarly, meerkats (*Suricata suricatta*) that were able to inhibit ineffective behavioural responses were more likely to solve tasks compared to individuals that persistently exhibited behaviours that did not lead to a solution (Thornton and Samson, 2012). Thus, habituation to a novel object/task, together with behavioural persistence and behavioural diversity/flexibility in responses to changing circumstances, may be critical factors in cognitive problem-solving abilities (Griffin and Guez, 2014).

The latency to consume the food was lowest in stage 1, because the mongooses did not have to open the lid of the puzzle box to obtain the food incentive. Stage 1, served as a habituation phase for the rest of the stages. In stage 2, the mongooses had to learn a new skill of flipping the lid open to obtain the food incentive. This represented a basic task where the mongooses needed to acquire the skills necessary to obtain the food incentive in the subsequent stages (i.e., opening the lid). The time taken for the mongooses to obtain the food incentive in stage 2 was, therefore, significantly greater compared to stage 1. In stage 3, when the stick was removed and the lid was completely closed, the latency to consume the food incentive was not significantly different compared to stage 2 even though stage 3 was experimentally more complex than stage 2. The similarity in the latency to consume between stage 2 and 3 may be due to the fact that, in stage 3 the mongooses had already acquired the foundational lid-opening ability and were able to quickly extend that knowledge and so were able to select behaviours that were known to previously aid in opening the box. In support of my findings, in a puzzle box task study in urban racoons (*Procyon lotor*), the latency of solving the problem decreased in subsequent trials as the racoons became more selective in their behavioural repertoire once they were familiar with the task (Daniels *et al.,* 2019). The similarity in latency to consume the food incentive in stage 2 and 3 indicates that the yellow mongooses could remember behavioural patterns that aid in success, were able to recall these behaviours and could then modify them according to the prevailing conditions of the new problem (Shettleworth, 1998). Furthermore, great apes that were repeatedly exposed to novel tasks over time were better at solving related tasks, this flexibility in cognitively developing new solutions to a previously exposed problem is therefore aided by a cumulative build-up of previously learnt information during individual learning (Manrique *et al.* 2013).

Stage 4 was the most complex stage where the mongooses were required to find a novel solution to open the puzzle box. In the first few trials of stage 4, in which, the mongooses attempted to open the box before removing the impediment but would persist

until the impediment fell off (i.e., trial-and-error learning), the mongooses then learnt to knock the impediment off before opening the lid before flipping the lid. Thus stage 4 required more trials as well as a change to the technique required to successfully complete the task and access the food incentive. Similarly, New Caledonian crows (C*orvus moneduloides*) presented with a novel feeding task were able to alter their behaviours and manipulate tools to suit the task requirements without prior learning experience (Bluff *et al*., 2007).

Frequency of behaviours

My second prediction was that with an increase in the complexity of the task, the yellow mongooses would exhibit a greater frequency of specific behaviours to access the food incentive, because the mongooses needed to engage with the device for longer. This was true for the frequency of digging. However, the frequency of investigating and vigilance decreased as the tasks became more complex.

Digging

The frequency of digging was lowest in stage 1 and increased as the complexity of the task increased. Yellow mongooses are primarily insectivorous in non-urban areas (Skinner and Chimimba, 2005), and may frequently use digging behaviours to search for insects. Yellow mongooses are considered "avid diggers" since mongooses were quite often seen digging at denning sites (presumably to open new holes; Cavallini 1993). Digging under the puzzle box would not result in the mongooses being able to flip open the lid of the puzzle box and so digging may be considered a displacement behaviour (Breed and Moore, 2015). Similarly, when testing problem-solving using multi-access puzzle boxes containing a food reward in redfronted lemurs (*Eulemur rufifrons*), individuals that were unsuccessful at accessing the reward were observed biting the box, showing signs of displacement since biting did not aid in solving the task (Huebner and Fichtel, 2015). Animals display displacement behaviours when they cannot attain a goal (Breed and Moore, 2015), such as in accessing a food incentive. In addition, the higher frequencies of digging could also represent signs of frustration. Frustration is defined as an animal's response to not being able to complete its goal or not receiving any incentive after having completed a task (Papini & Dudley, 1997). For example, in a study of primates, an increase in self-directed behaviours (e.g., scratching self-grooming) that were irrelevant to the behavioural context were linked to signs of frustration/anxiety (Maestripieri *et al*., 1992).

Overall, more digging might represent displacement or frustration, indicating that obtaining the food incentive may lead to motivational conflict. Motivational conflict arises when there are two opposing motivations (Richer, 1993). For example, the mongooses may have experienced a motivational conflict between giving up or continuing to attempt to access the food incentive. When chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) were given a choice between two options, a safe option with little reward and a risky option with a larger reward, individuals showed a variety of self-directed behaviours indicating signs of motivational conflict between the two choices (Rosati and Hare, 2013).

Investigating

Investigating behaviours, such as locomotion, sniffing, pawing, pushing, and pulling can increase an animal's knowledge of the solution to a problem (Benson-Amram and Holekamp, 2012). Animal species that exhibit greater investigation behaviours are known to be better innovators when presented with a novel task (Griffin and Guez, 2014). In Indian mynas (*Acridotheres tristis*), for example, individuals that made more goal-directed behaviours such as using their beaks to obtain the food incentive in a novel feeding task were more likely to reach a solution (Griffin *et al*., 2014). In the yellow mongooses, the frequency of investigating was much higher in stage 1 (open box stage; training phase) compared to the subsequent stages. These data show that the yellow mongooses were engaging with the puzzle box more frequently initially, most likely to overcome their fear and acquire knowledge about the puzzle box. In a similar puzzle box task, Carib grackles (*Quiscalus lugubris*) showed that reduced neophobia and increased habituation towards a novel object were highly correlated with increased exploratory behaviours (investigating) of the novel object and, through this, an increased likelihood of solving the problem (Overington *et al.,* 2011).

Vigilance

The frequency of vigilance decreased from stage 1 to stage 4 with the lowest frequency of vigilance in stage 4. Vigilance may hamper problem-solving because when an animal is being vigilant, more time must be invested in observing their surroundings and less on foraging (Chapman *et al.*, 2012) or in the case of my study, the mongoose finding a way to flip the lid of the puzzle box. The ability to focus on a specific goal is a critical mechanism for the processing of sensory information and decision-making (Budaev *et al*, 2019). Additionally, selective attention along with cognitive control (i.e., the organization and

integration of information from various sources), which prioritizes information for goal-directed decision-making, impacts the behavioural choices performed by the animal (Braver, 2012; Duncan, 2013; Mackie *et al*., 2013). Therefore, the mongooses may have reduced the number of times they were vigilant because their attention was directed to solving the puzzle box and gaining the food incentive, particularly in stage 4 because of the complexity of the task.

Behavioural transitions

My third prediction was that there would be greater behavioural transitions and SAB scores as the complexity of the tasks increased, since the mongooses needed to make different decisions about how to access the food incentive as the complexity of the task increased. The number and probability of behavioural transitions that occurred increased with changes in complexity across stages, except for stage 3 in the Nature Estate. As the mongooses became familiar with the puzzle box, they formed more pattern-like behavioural transitions. The SAB score in stage 3 was significantly lower compared to stage 4, but the SAB score for stage 2 was not significantly different compared to stage 3 and there was no significant difference between stage 2 and 4. These patterns indicate that as the mongooses spend more time interacting with the puzzle box, they became selective in their behaviours to solve the puzzle.

Living organisms are continuously exposed to a stream of stimuli and their behavioural responses to these stimuli are often the result of learning and recalling information (Rowan *et al*., 2001). However, to mount an appropriate response, an animal must not only learn which behaviours are appropriate but also how to produce the behaviours in a certain sequence (Rowan *et al*., 2001). Behavioural transitions were used to assess the overall patterns/sequence of behaviours performed by the yellow mongoose at each stage. To solve the puzzle box task, the yellow mongooses had to perform certain behaviours in a sequence, i.e., approach the puzzle box, find the position of the lid, and then flip the lid. This sequence, however, must be relatively fluid. For example, in stage 4, there was an extra step to obtaining the food incentive. The mongoose needed to first knock off the impediment before flipping the lid open. Therefore, the number of trials needed for the mongoose to efficiently learn the solution was the highest at stage 4.

In stage 2, there were a few significant transitions between behaviours, indicating that the behavioural sequences were comparatively randomly organised. The mongooses solved the problem quicker or reached the outcome faster indicating that flipping the lid was easier

for the mongoose in stage 2 compared to subsequent stages. Therefore, it would be less likely to observe many significant patterns at stage 2. However, as the complexity of opening the puzzle box increased, the number of significant behavioural transitions increased, showing that the mongooses were using a less random sequence to solve the puzzle box. Mongooses were likely engaging in more routine-like behaviours in more complex stages (Schwaibold and Pillay, 2006). For example, there was a significant transition between sniffing and locomotion in stages 2-4, but these transitions were bidirectional in stages 3 and 4, indicative of routine behavioural sequences (Schwaibold and Pillay, 2006). For instance, in capuchin monkeys (*Cebus apella*) and chimpanzees (*Pantroglodytes*), learning abilities were tested by simulating natural sequential feeding behaviours (Conway and Christiansen, 2001). Individuals were able to learn a fixed sequence of behaviours and were able to learn a more complex sequence to obtaining the food reward (Conway and Christiansen, 2001). The ability to learn and recall a sequence of behaviours may be indictive of a species cognitive ability (Rowan *et al*., 2001).

In my study, the mongooses transitioned from digging under the puzzle box to being vigilant, a pattern observed from stage 2 to stage 4. The transition between these behaviours did not aid in the mongooses flipping open the lid. Instead, the behavioural transition from digging to vigilance was likely to disrupt the process of opening of the box. Therefore, the routine observed between digging and vigilance (i.e., stop to observe the surrounding environment) suggests that the mongooses stopped engaging with the goal and engaged with another task, possibly due to frustration (see above).

Matrix correlation

Several correlations between the stages and location are significant which indicates that while there are differences in transition between stages and location, the overall patterns are similar. It seems as though the mongooses are making different transitions by stage and location, but they are building on the broad transitions from the previous stage, regardless of location – which may indicate how learning occurs. The mongooses are using foundational information and building on this to meet the new task. A study testing problem solving using task that increased in complexity in redfronted lemurs (*Eulemur rufifrons*) showed that individuals that were successful in solving each level of complexity did so by expanding on skills learned in previous stages (Huebner and Fichtel, 2015). Therefore, the ability to learn from previous experience and adapt behavioural responses to the current situation may be key in appropriate decision making during problem solving (Huebner and Fichtel, 2015).

SAB Score

SAB scores indicate the level of preservation in behaviours rather than the frequency of occurrence of behaviours (Jones *et al*., 2011) or broader behavioural transitions. SAB scores are usually used to test the spatial working memory of non-human animals (Lewis *et al.,* 2017) and considers an animal's ability to temporally store spatial information from environmental cues (Lewis *et al.,* 2017). The ability to store and retrieve memories is likely to influence an individual's moment-by-moment decision making. The SAB score showed whether the mongooses were able to select behaviours that led to opening the puzzle box more often than those that did not. A lower SAB score suggests repetitive behaviours, whereas a high SAB score shows more random behaviours observed in a moment-by-moment sequence (Jones *et al*., 2011). There was no significant difference in the SAB scores between stages 2 and 4 which was higher compared to stage 3, indicating that the mongooses were following the same patterns of behaviours in a moment-by-moment sequence. Stage 2 and 4 seemed to be the complex problem-solving stages for the yellow mongooses as also indicated by the greater latency to consume the food incentive and the frequency of behaviours. In stage 2, the mongoose alternated most often between behaviours such as locomotion, sniffing, vigilance, digging and occasionally pawing at the box. A similar repertoire of behaviours was observed in stage 3. However, in stage 4, the mongooses were performing more behaviours (locomotion, sniffing, vigilance digging) in a slightly less random sequence, possibly because they had become familiar with the puzzle box and were able to select behavioural patterns that are best suited to opening the box.

Comparison between locations of varying levels of anthropogenic disturbance

My fourth prediction was that the latency to consume, frequency of behaviours, behavioural transitions and SAB scores would differ between the less urbanised area than the more urbanised area. The latency to consume the food incentive and the frequency of investigating the puzzle box and vigilance were higher in the Eco Estate compared to the Nature Estate; there was no significant difference in the frequency of digging between the two locations. The number of significant transitions for stages 2 and 3 was higher in the Eco Estate compared to the Nature Estate but the number of significant transitions for stage 4 was higher in the Nature Estate compared to the Eco Estate. The SAB score was higher in the Eco Estate compared to the Nature Estate.

The latency to consume the food incentive was significantly higher in the Eco Estate compared to the Nature Estate, indicating that the yellow mongooses in the Nature Estate

were quicker to flip the lid and obtain the food incentive. In addition, while the frequency of digging did not differ significantly across locations, the frequency of investigating behaviours was significantly higher in the Nature Estate compared to the Eco Estate. The frequency of vigilance was significantly higher in the Eco Estate compared to the Nature Estate.

For example, urban populations of Eurasian red squirrels (*Sciurus vulgaris*) had shorter FID (Flight Initiation Distance) and were less vigilant when a human approached, indicating that the urban population had habituated to humans (Uchida *et al.,* 2019). Similar findings were reported in cottontail rabbits (*Sylvilagus floridanus;* Lima *et al*., 2021).

Therefore, animals living in urban environments are less likely to be vigilant compared to their rural counterparts, likely due to their habituation to people and the reduced likelihood of predation (Chapman *et al.*, 2012). In contrast, my results could possibly be due to the presence of people, suggesting that the mongooses were more disturbed in the Eco Estate because of the presence of people or domestic pets in the vicinity. Anthropogenic disturbance can increase stress in animals (Partecke *et al*., 2006; Hammond *et al*., 2019) which generally has a negative impact on cognitive abilities (McEwen and Sapolsky, 1995). Therefore, mongooses may have been more disturbed in the Eco Estate due to the anthropogenic disturbance and may have impacted its moment-by-moment decision making. The behavioural transitions were highly correlated between the Eco Estate and the Nature Estate, indicating similar broad-scale decision-making patterns. However, the SAB scores were higher in the Eco Estate, indicating behaviours were less random compared to the Nature Estate.

The variation in decision making behaviours displayed by the yellow mongooses may be attributed to other environmental conditions that were not accounted for in this study such as hunger levels (Johnson-Ulrich *et al*., 2021). The mongooses in the Eco Estate may have more ready access to anthropogenic food sources compared to the Nature Estate and therefore may be less motivated to obtain the food incentive. Spotted hyena *(Crocuta crocuta*) in urban areas in which anthropogenic food sources are more readily available showed signs of reduced innovativeness compared to less urbanised areas (Johnson-Ulrich *et al*., 2021).

Conclusion

I found that yellow mongooses in the Nature Estate employed new behavioural strategies with greater task complexity that led to the opening of the puzzle box and rejected strategies that did not, in contrast to the mongooses in the Eco Estate. I found that the yellow mongooses were able to modify their decision-making through learning and became more

efficient in response to the challenge of opening the puzzle box at each level of complexity. Stages were not equally challenging as evidenced by variation in behaviours and the latency to consume the food incentive of each stage, (i.e., stage 4 was experimentally more complex compared to the other the stages). The different level of complexity allowed me to assess the variation in decision making as the task increased in complexity.

Future studies should consider testing inherent differences, such as sex, age, personality traits (aggression, bolder temperament, tameness). Furthermore, social learning vs asocial learning would provide a finer measurement of the mechanisms used during learning and decision making employed by the yellow mongooses. In addition, a detailed analysis of each trial could provide an assessment of the learning process itself, which was beyond the scope of my study. I employed a sequential design of increasing complexity to provide the mongooses with opportunities to habituate to the novel puzzle box. During the interactions with the puzzle box the mongoose learned and developed a new skill i.e. opening the lid of the puzzle box. Other basic skills could be developed depending on the study or the implementation of a differently designed puzzle box. A future study could employ a random design to test the extent of innovation, problem-solving and decision-making without incrementally learning; this could be done by dishabituating the yellow mongoose to the puzzle box and then setting up stage 4 of the experiment and observing their behaviours. Furthermore, behavioural motivation may be a major factor in how fast an individual makes a decision. For example, an individual that solves a task faster than its conspecific may simply be more motivated (food deprivation and body conditions) rather than more cognitive and therefore the variation in individual motivation should be considered in future studies (Griffin and Guez, 2016). The environment in which the animal lives in has an impact on the decision-making process for example in this study individuals in less urbanised areas performed better at problem solving and developed better decision making skills compared to individuals in more urbanised areas. A comparison between urban and rural populations would give a better insight into decision making of yellow mongooses under different predation risks and/or food availability.

Reference list

Audet, J.N., Ducatez, S. and Lefebvre, L., 2016. The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, *27*, pp.637-644.

Auersperg, A.M., Von Bayern, A.M., Gajdon, G.K., Huber, L. and Kacelnik, A., 2011. Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PloS One*, *6*, p.e20231.

Bateman, P.W. and Fleming, P.A., 2012. Big city life: carnivores in urban environments. *Journal of Zoology*, *287*, pp.1-23.

Bateson, P.P.G., 1983. *Mate choice*. Cambridge University Press. Cambridge.

Bebus, S.E., Small, T.W., Jones, B.C., Elderbrock, E.K. and Schoech, S.J., 2016. Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Animal Behaviour*, *111*, pp.251-260.

Benson-Amram, S. and Holekamp, K.E., 2012. Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*, pp.4087-4095.

Benson-Amram, S., Weldele, M.L. and Holekamp, K.E., 2013. A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour*, *85*, pp.349-356.

Berman, G.J., Bialek, W. and Shaevitz, J.W., 2016. Predictability and hierarchy in Drosophila behavior. *Proceedings of the National Academy of Sciences*, *113*, pp.11943-11948.

Bhat, A., Greulich, M.M. and Martins, E.P., 2015. Behavioral plasticity in response to environmental manipulation among zebrafish (*Danio rerio*) populations. *PLoS One*, *10*, p.e0125097.

Bluff, L. A., Weir, A. A. S., Rutz, C., Wimpenny, J. H., & Kacelnik, A., 2007. Tool-related cognition in New Caledonian crows. *Comparative Cognition & Behavior Reviews, 2*, pp.1-25.

Blumstein, D.T. and Bouskila, A., 1996. Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos*, pp.569-576.

Braver, T.S., 2012. The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, *16*, pp.106-113.

Breed, M.D. and Moore, J., 2015. 'Homeostasis and Time Budgets' in *Animal behavior*, second edition. Academic Press, pp. 109-114.

Brewer, G.D. & Stern, P.C., 2005. *Decision making for the Environment Social and Behavioral Science Research Priorities*, Washington, DC: National Academies Press

Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S. and Giske, J., 2019. Decision-making from the animal perspective: bridging ecology and subjective cognition. *Frontiers in Ecology and Evolution*, *7*, p.164.

Casarrubea, M., Sorbera, F. and Crescimanno, G., 2008. Multivariate analysis of the modifications induced by an environmental acoustic cue on rat exploratory behavior. *Physiology & behavior*, *93*, pp.687-696.

Cavallini, P., 1993. Spatial organization of the yellow mongoose *Cynictis penicillata* in a coastal area. *Ethology ecology & evolution*, *5*, pp.501-509.

Chapman, T., Rymer, T. and Pillay, N., 2012. Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris. Naturwissenschaften*, *99*, pp.893-902.

Chittka, L., Skorupski, P. and Raine, N.E., 2009. Speed–accuracy trade-offs in animal decision making. *Trends in Ecology & Evolution*, *24*, pp.400-407.

Chow, P.K.Y., Clayton, N.S. and Steele, M.A., 2021. Cognitive performance of wild Eastern grey squirrels (*Sciurus carolinensis*) in rural and urban, native and non-native environments. *Frontiers in Ecology and Evolution*, *9*, pp.80.

Conway, C.M. and Christiansen, M.H., 2001. Sequential learning in non-human primates. *Trends in cognitive sciences*, *5*, pp.539-546.

Cronk, N.E. and Pillay, N., 2019. Flexible use of urban resources by the yellow mongoose C*ynictis penicillata*. *Animals*, *9*, pp.447.

Cronk, N.E., Pillay, N., 2018. Food choice and feeding on carrion in two African mongoose species in an urban environment. *Acta Ethol 21*, pp.127-136.

Cuthill, I. and Kacelnik, A., 1990. Central place foraging: a reappraisal of the 'loading effect'. *Animal Behaviour*, *40*, pp.1087-1101.

Daniels, S.E., Fanelli, R.E., Gilbert, A. and Benson-Amram, S., 2019. Behavioral flexibility of a generalist carnivore. *Animal cognition*, *22*, pp.387-396.

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

Dukas, R. and Morse, D.H., 2003. Crab spiders affect flower visitation by bees. *Oikos*, *101*, pp.157-163.

Dukas, R., 2004. Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution and Systems.*, *35*, pp.347-374.

Duncan, J., 2013. The structure of cognition: attentional episodes in mind and brain. *Neuron*, *80*, pp.35-50.

Fawcett, T.W., Fallenstein, B., Higginson, A.D., Houston, A.I., Mallpress, D.E., Trimmer, P.C. and McNamara, J.M., 2014. The evolution of decision rules in complex environments. *Trends in Cognitive Sciences*, *18*, pp.153-161.

Fawcett, T.W., Hamblin, S. and Giraldeau, L.A., 2013. Exposing the behavioral gambit: the evolution of learning and decision rules. *Behavioral Ecology*, *24*, pp.2-11.

Franks, N.R., Dornhaus, A., Fitzsimmons, J.P. and Stevens, M., 2003. Speed versus accuracy in collective decision making. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*, pp.2457-2463.

Gajdon, G.K., Fijn, N. & Huber, L. 2006. Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Animal Cognition*. 9, pp.173-181.

Geffroy, B., Samia, D.S., Bessa, E. and Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, *30*, pp.755-765.

Gehrt, S.D., 2007. Ecology of coyotes in urban landscapes. In *Wildlife Damage Management Conferences Proceedings,* pp. 63.

Gigerenzer, G. and Gaissmaier, W., 2011. Heuristic decision making. *Annual review of Psychology*, *62*, pp.451-482.

Gonzalez-Bellido, P.T., Fabian, S.T., Nordström, K., 2016. Target detection in insects: optical, neural and behavioral optimizations. *Current Opinion in Neurobiology, 41*, pp.122–128.

Goumas, M., Lee, V.E., Boogert, N.J., Kelley, L.A. and Thornton, A., 2020. The role of animal cognition in human-wildlife interactions. *Frontiers in Psychology*, *11*, pp.3019.

Greenberg, R.S., 2003. The role of neophobia and neophilia in the development of innovative behaviour of birds. *Animal Innovation*.

Griffin, A.S. and Guez, D., 2014. Innovation and problem solving: a review of common mechanisms. *Behavioural Processes*, *109*, pp.121-134.

Griffin, A.S., Diquelou, M. and Perea, M., 2014. Innovative problem solving in birds: a key role of motor diversity. *Animal Behaviour*, *92*, pp.221-227.

Hammond, T.T., Vo, M., Burton, C.T., Surber, L.L., Lacey, E.A. and Smith, J.E., 2019. Physiological and behavioral responses to anthropogenic stressors in a human-tolerant mammal. *Journal of Mammalogy*, *100*, pp.1928-1940.

Hauser, M.D., 1999. Perseveration, inhibition and the prefrontal cortex: a new look. *Current Opinion in Neurobiology*, *9*, pp.214-222.

Hendry, A.P., Farrugia, T.J. and Kinnison, M.T., 2008. Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*, pp.20-29.

Huebner, F. and Fichtel, C., 2015. Innovation and behavioral flexibility in wild redfronted lemurs (*Eulemur rufifrons*). *Animal Cognition*, *18*, pp.777-787.

Hughes, R.N., 2004. The value of spontaneous alternation behavior (SAB) as a test of retention in pharmacological investigations of memory. *Neuroscience & Biobehavioral Reviews*, *28*, pp.497-505.

Jelbert, S.A., Taylor, A.H. and Gray, R.D., 2015. Investigating animal cognition with the Aesop's Fable paradigm: Current understanding and future directions. *Communicative & Integrative Biology*, *8*, pp. e1035846.

Johnson-Ulrich, L., Yirga, G., Strong, R.L. and Holekamp, K.E., 2021. The effect of urbanization on innovation in spotted hyenas. *Animal Cognition*, *24*, pp.1027-103

Jones, M.A., Mason, G.J. and Pillay, N., 2011. Correlates of birth origin effects on the development of stereotypic behaviour in striped mice, *Rhabdomys*. *Animal Behaviour*, *82*, pp.149-159.

Kacelnik, A. and Marsh, B., 2002. Cost can increase preference in starlings. *Animal Behaviour*, *63*, pp.245-250.

Kandel, E.R. and Hawkins, R.D., 1992. The biological basis of learning and individuality. *Scientific American*, *267*, pp.78-87.

Kendal, R.L., Coe, R.L. and Laland, K.N., 2005. Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *66*, pp.167-188.

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. Bloomsbury, London, pp. 334-339.

Kohn, J.R., Heath, S.L. and Behnia, R., 2018. Eyes matched to the prize: the state of matched filters in insect visual circuits. *Frontiers in Neural Circuits*, *12*, pp.26.

Kummer, H. and Goodall, J., 1985. Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*, pp.203-214.

Le Roux, A., Cherry, M.I., Gygax, L., Manser, M.B., 2009. Vigilance behaviour and fitness consequences: comparing a solitary foraging and an obligate group-foraging mammal. *Behavioural Ecology Sociobio*logy 63, 1097-1107.

Lee, V.E. and Thornton, A., 2021. Animal cognition in an urbanised world. *Frontiers in Ecology and Evolution*, *9*, pp.120.

Lewis, S. A., Negelspach, D. C., Kaladchibachi, S., Cowen, S. L., & Fernandez, F., 2017. Spontaneous alternation: A potential gateway to spatial working memory in Drosophila. *Neurobiology of Learning and Memory*, *142*, pp.230–235.

Lima, S.L. and Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, pp.619-640.

Lima, S.L., 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia*, *66*, pp.60-67.

Lima, S.L., Gámez, S., Arringdale, N. and Harris, N.C., 2021. Vigilance response of a key prey species to anthropogenic and natural threats in Detroit. *Frontiers in Ecology and Evolution*, *9*, pp.1.

Łopucki, R. and Kitowski, I., 2017. How small cities affect the biodiversity of ground-dwelling mammals and the relevance of this knowledge in planning urban land expansion in terms of urban wildlife. *Urban Ecosystems*, *20*, pp.933-943.

Lowry, H., Lill, A. and Wong, B.B., 2013. Behavioural responses of wildlife to urban environments. *Biological Reviews*, *8*3, pp.537-549.

Mackie, M.A., Van Dam, N.T. and Fan, J., 2013. Cognitive control and attentional functions. *Brain and Cognition*, *82*, pp.301-312.

Maestripieri, D., Schino, G., Aureli, F. and Troisi, A., 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*, pp.967-979.

Mangel, M. and Clark, C.W., 1986. Towards a unifield foraging theory. *Ecology*, *67*, pp.1127-1138.

Marsh, B., 2002. Do animals use heuristics? *Journal of Bioeconomics*, *4*, pp.49-56.

Mazza, V., Eccard, J.A., Zaccaroni, M., Jacob, J. and Dammhahn, M., 2018. The fast and the flexible: cognitive style drives individual variation in cognition in a small mammal. *Animal Behaviour*, *137*, pp.119-132.

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

McEwen, B.S. and Sapolsky, R.M., 1995. Stress and cognitive function. *Current opinion in Neurobiology*, *5*(2), pp.205-216.

McKinney, M.L., 2002. Urbanization, Biodiversity, and Conservation. The impacts of urbanization on native species are poorly studied but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*, *52*, pp.883-890.

McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, pp.247-260.

McNamara, J.M. and Houston, A.I., 1986. The common currency for behavioral decisions. *The American Naturalist*, *127*, pp.358-378.

Møller, A. 2008. Flight distance of urban birds, predation, and selection for urban life. *Behavioural Ecology and Sociobiology*, 63, pp.63-75.

O'Donnell, K. and del Barco-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*, pp. juaa014.

Overington, S.E., Cauchard, L., Côté, K.A. and Lefebvre, L., 2011. Innovative foraging behaviour in birds: what characterizes an innovator? *Behavioural Processes*, *87*, pp.274-285.

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, pp.32-48.

Papini, M.R. and Dudley, R.T., 1997. Consequences of surprising reward omissions. *Review of General Psychology*, *1*, pp.175-197.

Partecke, J., Schwabl, I. and Gwinner, E., 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. *Ecology*, *87*, pp.1945-1952.

Partridge, L. 1978. Habitat selection. - In: Krebs, J. R. and Davies, N. B. (eds), Behavioural ecology: an evolutionary approach. Blackwell, London, pp. 351-376.

Raine, N.E. and Chittka, L., 2012. No trade-off between learning speed and associative flexibility in bumblebees: a reversal learning test with multiple colonies. *PLoS One*, *7*(9).

Ramsey, G., Bastian, M.L. & van Schaik, C. 2007. Animal innovation defined and operationalized. *Behavioral and Brain Sciences,30*, pp. 393-437.

Reader, S.M. and Laland, K.N. eds., 2003. *Animal Innovation* (Vol. 10). Oxford: Oxford University Press.

Rebolo-Ifrán, N., Carrete, M., Sanz-Aguilar, A., Rodríguez-Martínez, S., Cabezas, S., Marchant, T.A., Bortolotti, G.R. and Tella, J.L., 2015. Links between fear of humans, stress and survival support a non-random distribution of birds among urban and rural habitats. *Scientific Reports*, *5*, pp.1-10.

Richer, J., 1993. Avoidance behavior, attachment, and motivational conflict. *Early Child Development and Care*, *96*, pp.7-18.

Rochais, C., Maille, A., Jäger, J., Pillay, N., Schradin, C., 2019. How does cognitive performance change in relation to seasonal and experimental changes in blood glucose levels? *Animal Behaviour,* 158, pp. 149-159.

Rosati, A.G. and Hare, B., 2013. Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PloS One*, *8*(5), pp. e63058.

Rothacher, Y., Nguyen, A., Lenggenhager, B., Kunz, A. and Brugger, P., 2020. Walking through virtual mazes: Spontaneous alternation behaviour in human adults. *Cortex*, *127*, pp.1-16.

Rowan, J.D., Fountain, S.B., Kundey, S. and Miner, C.L., 2001. A multiple species approach to sequential learning: Are you a man or a mouse? *Behavior Research Methods, Instruments, & Computers*, *33*, pp.435-439.

Samia, D.S., Nakagawa, S., Nomura, F., Rangel, T.F. and Blumstein, D.T., 2015. Increased tolerance to humans among disturbed wildlife. *Nature Communications*, *6*, pp.8877.

Schradin, C. and Pillay, N., 2005. Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammalian Biology*, *70*, pp.84-92.

Schwaibold, U. and Pillay, N., 2006. Behavioral strategies of the African ice rat *Otomys sloggetti robertsi* in the cold. *Physiology & behavior*, *88*, pp.567-574.

Shettleworth, S.J., 1998. Cognition, evolution, and behavior. Oxford University Press, New York.

Sih A. 2004. A behavioral ecological view of phenotypic plasticity. In: Dewitt TJ, Scheiner SM editors. *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford: Oxford University Press. pp.112-125.

Sih, A. and Del Giudice, M., 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, pp.2762-2772.

Sih, A., 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, *85*, pp.1077-1088.

Sih, A., Ferrari, M.C. and Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*, pp.367-387.

Skinner, J.D. and Chimimba, C.T., 2005. *The Mammals of the Southern African Sub-region*. Cambridge University Press.

Sol, D., 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, *5*, pp.130-133.

Sol, D., Griffin, A.S. and Bartomeus, I., 2012. Consumer and motor innovation in the common myna: the role of motivation and emotional responses. *Animal Behaviour*, *83*, pp.179-188.

Sol, D., Griffin, A.S., Bartomeus, I. and Boyce, H., 2011. Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS One*, *6*, pp. e19535.

Sol, D., Lapiedra, O. and González-Lagos, C., 2013. Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*(5), pp.1101-1112.

Spruijt, B.M. and Gispen, W.H., 1984. Behavioral sequences as an easily quantifiable parameter in experimental studies. *Physiology & Behavior*, *32*, pp.707-710.

Staddon, J.E.R., 2016. *Adaptive Behavior and Learning*. Cambridge University Press.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. - Princeton Univ. Press, Princeton, NJ.

Ten Berge, T. and Van Hezewijk, R., 1999. Procedural and declarative knowledge: An evolutionary perspective. *Theory & Psychology*, *9*, pp.605-624.

Thanh, P.D., Wada, K., Sato, M. and Shirayama, Y., 2003. Decorating behaviour by the majid crab *Tiarinia cornigera* as protection against predators. *Journal of the Marine Biological Association of the United Kingdom*, *83*, pp.1235-1237.

Thornton, A. and Samson, J., 2012. Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*, pp.1459-1468.

Tinbergen, J.M., 1981. Foraging decisions in starlings (*Sturnus vulgaris L.*). *Ardea*, *55*, pp.1-67.

Tuxbury, S.M. and Salmon, M., 2005. Competitive interactions between artificial lighting and natural cues during sea finding by hatchling marine turtles. *Biological Conservation*, *121*, pp.311-316.

Uchida, K., Suzuki, K.K., Shimamoto, T., Yanagawa, H. and Koizumi, I., 2019. Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behavioral Ecology*, *30*, pp.1583-1590.

Webster, S.J. and Lefebvre, L., 2001. Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, *62*, pp.23-32.

Wong, B. and Candolin, U., 2015. Behavioral responses to changing environments. *Behavioral Ecology*, *26*, pp.665-673.

Yokoi, T. and Fujisaki, K., 2009. Hesitation behaviour of hoverflies *Sphaerophoria spp*. to avoid ambush by crab spiders. *Naturwissenschaften*, *96*, pp.195-200.

Yoo, S.B.M., Hayden, B.Y. and Pearson, J.M., 2021. Continuous decisions. *Philosophical Transactions of the Royal Society B*, *376*, pp.20190664.