Individual differences in cognitive abilities and task performance in wild chacma baboons (*Papio ursinus*)

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Cover Photo: Tanganyika, daughter of Yaoundé, but most importantly, sister of Porto Novo. Named after the African Great Lake where *Neolamprologus pulcher* is found. Photo credit: Claudia Martina (C.M.)

Declaration of originality

I, Claudia Martina, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Claudia Martina, April 2019

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Abstract

Animal species vary widely in their cognitive abilities. However, relatively few studies, particularly in wild conditions, have assessed cognitive differences between individuals within a species, even when such differences may impact individual fitness. In this thesis, I investigate variation in the cognitive abilities and task performance of individuals belonging to two troops of wild chacma baboons (*Papio ursinus*) in Namibia. I conducted three field experiments to assess individual variation in associative learning abilities, using an operant conditioning task, an extractive foraging task and a second-order conditioning task (Chapters 4-6). I then used these same tasks to explore individual differences in both task participation and the use of different foraging techniques (Chapters 7-8). In each chapter I also sought to test evolutionary hypotheses about that variation according to individual phenotype, including age, sex and social rank. I found little evidence that the baboons learnt the intended associations as initially predicted in the three tasks, and likewise little evidence of individual differences in learning ability that could be related to phenotype in the two tasks in which I was able to explore this. However, I did find consistent individual differences in task participation and feeding techniques. Overall, my findings highlight both, the challenges and opportunities of conducting tests in the wild.

Impact Statement

This thesis, focusing on the individual differences in cognitive abilities in chacma baboons, impacts on two relevant areas.

First, the research presented here makes a point of testing untrained individuals in their natural habitat with ecologically-relevant tasks. This is important, as much of the past research evaluating cognition in animals has been restricted to the captive environment, where animals are trained extensively, constrained by the environment in which they are kept, and tested with tasks that do not represent their natural behaviour. My experiments deal with this limitation by testing wild animals that remained free to conduct normal activities while being naïve and untrained prior to being tested. Such a methodology could be expanded to include other species in wild conditions to understand how cognitive mechanisms, particularly those associated with learning, vary and evolve.

Second, across Africa, baboons are considered a nuisance species. The flexibility of baboon behaviour puts them in direct conflict with farmers and tourists, as well as urban dwellers when harsh environmental conditions, such as droughts, push them into urban areas. Recently, simple cognitive training techniques, similar to the ones I use here, have been proposed as a way to ameliorate such conflicts. Training animals to respond to, or avoid, certain stimuli, for example, could not only provide a reliable way in which to protect crops and infrastructure, but potentially ensure the safety of animals across their range in a non-invasive way. My research provides a first step towards understanding the sorts of stimuli to which nuisance species such as baboons are likely to respond, as well as the conditions under which they are likely to do so. More importantly, in a social species, key behaviours have the potential to spread across a population through social learning; therefore, identifying those individuals who are first to respond and learn novel stimuli, as my research does, may assist in the design of effective management plans.

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Chapter 1

1.1. INTRODUCTION

The term “cognition” is commonly used to describe the process through which information from the environment is acquired, stored and used (Shettleworth, 2010). Since it was first studied, cognition was, and still is, difficult to define and measure. However, one approach has been to look at common mechanisms, generally termed “cognitive abilities”, to determine how organisms process information from their environment (Shettleworth, 2010). In the 1960s, based on the Darwinian idea that animals share common cognitive abilities with humans but possess them to a less-developed extent, comparative psychologists sought to explain cognition on an evolutionary scale based on the phylogenetic relatedness of various animal species to humans (Healy et al., 2009). Because of this largely-anthropocentric view, experiments on a wide range of species were conducted under laboratory conditions (Balda et al., 1998; Ristau, 1992), ironically revealing unexpected cognitive abilities in animals (Balda et al., 1998). Gallup (1969), for instance, described what he considered as self-awareness when he presented a mirror to chimpanzees (*Pan troglodytes*) who used the mirror to identify a mark on their face, an ability previously thought to be uniquely human.

Classical ethology—the study of animal behaviour—developed because researchers wanted to gather empirical and observational evidence about animals that went beyond the anthropocentrism that dominated the field of comparative psychology (Allen & Bekoff, 1997). Over time, studies began focusing on the adaptive value and evolution of behaviour, developing into the field of behavioural ecology (Shettleworth, 2010). The integration of cognitive principles to the evolution and ecology of naturally occurring behaviours (Real, 1993) was later referred to as *cognitive ecology*, which focused on the cognitive adaptations of a species or individuals to their environment (Mettke-Hofmann, 2014). Broadly, cognitive ecology hypothesises that environmental challenges select for behavioural adaptations related to cognition (Shettleworth, 2010). While this field was formally defined by Le Real in 1993, evidence for it was reported as early as 1990, when studies evaluated the relationship between the hippocampus and spatial abilities in food-caching in birds (Krebs et al., 1990).

It is now commonly accepted that animals possess abilities previously thought to be characteristic of humans, from complex forms of communication (Snowdon & Boe, 2003), to problem-solving and tool use (Kummer & Goodall, 1985). One persistent question still outstanding in the field is whether such behaviours are performed in a state of consciousness (Ristau, 1992). One of the main arguments of cognitive ethology, a field analogous to cognitive ecology which favours behavioural observations, is that animals are not simply acting in response to environmental cues but rather that they consciously select and act on previous information (Ristau & Marler, 1991), particularly when faced with novel challenges (Griffin, 1998). Unfortunately, such arguments are still limited to behavioural and anecdotal observations. However, no matter how the study of animal cognition is addressed, the principle is the same: cognitive abilities are determined and developed according to the ecological pressures animals experience in a given environment, where their behaviour evolves accordingly (Shettleworth, 2010).

1.2. THESIS AIMS AND STRUCTURE

Despite its importance for individual fitness, and perhaps due to the history of comparative studies in captivity, two aspects of cognition have often been overlooked: the individual variation found within a population; and the effect of the test setting, i.e., a wild versus captive environment, on individual performance. In light of these poorly understood aspects of cognition, the aims of this thesis are threefold:

(1) to investigate individual differences in the cognitive abilities of animals;

(2) to determine whether and which individual traits may influence these abilities;

(3) to explore some of the issues that might explain differences in cognitive performance between captive and wild settings.

To this end, I presented individuals in two groups of wild chacma baboons (*Papio ursinus*) with three cognitive tasks to quantify patterns of variation in task performance, as well as to test a suite of hypotheses about how such variation might arise as a result of differences in phenotypic traits and states. Chacma baboons were chosen as a model species for this work because, as a robust terrestrial primate species, they are tractable for field experiments and their individual characteristics, together with their social and physical environment, can be easily quantified.

Following this brief introductory chapter (*Chapter 1*), my thesis adopts the following structure:

Chapter 2 expands on the topic of cognition that I started in this chapter. Specifically, it introduces the concept of individual differences in cognition and provides a literature review of the phenotypic traits and states that might drive such variation. Additionally, this chapter details the differences between cognitive studies in captivity and in the wild, including how the testing environment and general methodology used in captivity has the potential to affect how animals approach and solve cognitive tasks.

Chapter 3 introduces the study system, providing background information on the study species (chacma baboons); the study site in Namibia (Tsaobis Nature Park); the day-to-day data collection; and general details of the experimental protocols used in the next chapters. Building on the information presented in the preceding chapter, I also outline my five ‘core’ hypotheses relating cognitive ability to phenotype that I set out to test in the following three chapters.

Chapter 4 presents a first test of cognition in wild baboons, using a simple associative learning task. This task involved learning an association between colour and taste cues using coloured corn kernels, some of which were made unpalatable with a bitter substance. I also test my core hypotheses regarding the role of individual phenotype on task performance.

Chapter 5 involves a second test of associative learning using an extractive foraging task, where the reward associated to each cue differs in value. This task involved learning an association where the cost of making an incorrect choice between two coloured paper bags is higher since a valuable reward can be lost. I also test my ‘core’ hypotheses regarding the link between cognitive abilities and individual phenotype.

Chapter 6 investigates a third aspect of associative learning, second-order conditioning, which involves linking associations among several stimuli. In particular, it evaluates the ability of baboons to successfully associate a neutral stimulus with an auditory cue previously paired with a food reward over three distinct phases.

Chapter 7 investigates differences in the motivation of individuals to participate in a task, including the likelihood/latency to interact with the tasks and their subsequent degree of exploration. Specifically, I examine the patterns of task participation in Chapters 5 and 6 to test four hypotheses about what might generate differences in individuals' motivation, namely the availability of competing activities, information use preferences (personal or social), exposure to immediate stressors, and individual phenotypic variation.

Chapter 8 investigates individual variation in the foraging techniques used in each task, focusing on the mechanical manipulations and physical postures that individuals adopted during the tasks described in Chapters 5 and 6. Specifically, I evaluate whether a given technique might affect an individual's ability to conceal its food discovery from others and/or to eat more quickly, and whether individuals varied in their use of these techniques depending on their age and social rank, and their experience of aggression in the previous trial.

Chapter 9 concludes my thesis with a discussion of my findings across chapters, summarising and synthesising my key results, and exploring their wider implications.

Chapter 2

Individual Differences In Cognition: Phenotypic Correlates And The Problems Of Captive Testing

2.1 ABSTRACT

Defining and measuring cognitive mechanisms is difficult. To understand how cognitive traits have evolved, previous studies have traditionally focused on interspecific differences. As a result, intraspecific variation, which is likely to be associated with fitness differences, has been neglected. There are a number of potential determinants of individual cognitive variation, from genetic effects and early-life environment to phenotypic traits and states. In spite of the significance of testing variation in a natural environment, the study of animal cognition has been largely restricted to the captive environment, as it allows researchers to control for ecological and social aspects that might confound the animal's performance. The present chapter introduces and describes five key phenotypic traits/states (sex, age, social rank, personality and risk assessment) which may be important determinants of variation in cognitive abilities. Here as well, I discuss how the nature of captive studies may affect how cognitive variation is measured and limit the generisability of their findings to wild conditions.

2.2 INTRODUCTION

Cognition refers to the acquisition, processing and use of information obtained from the environment (Dukas, 2004; Shettleworth, 2010). Key mechanisms or “abilities” by which a proximate measure of cognition is possible include memory, learning and problem-solving, to name a few (Shettleworth, 2010). Such abilities can be further divided into sub-categories (e.g. learning can involve social learning, associative learning, discrimination learning: Griffin & Healy) that allow us to further clarify the cognitive processes involved. Learning for instance, broadly results from past experiences which allow animals to adjust their behaviour accordingly (Shettleworth, 2010); while associative learning, one of the most common types of learning, specifically involves the association of different sensory stimuli (Ginsburg & Jablonka, 2010; Shettleworth, 2001). Such sensory stimuli may include colour cues – commonly used to test associative learning in experiments with birds (hummingbirds, *Selasphorus rufus*: Samuels et al., 2014) and insects (bumble-bees, *Bombus flavifrons*: Dukas & Waser, 1994; *Bombus terrestris*: Ings et al., 2009) because they are used by animals during foraging to discriminate between rewarding and non-rewarding flowers.

Historically, research on animal cognition has largely focused on characterizing interspecific differences to understand the processes by which a given cognitive ability evolves (Herrmann & Call, 2012; MacLean et al., 2012; Papini, 2002). Such research was initially limited primarily to comparing the cognitive abilities of species within the Primate order (Kanngiesser & Call, 2010; Schmitt et al., 2012) due to the anthropocentric focus of comparative psychology and the life-history traits that non-human primates share with humans. Herrmann et al. (2007), for example, compared the cognitive skills of children with those of chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). Recently, interspecific comparisons of cognitive ability have been extended to other taxa that share, with primates, the social challenges of group living, for instance birds (Obozova et al., 2014) and dogs (Miklósi et al., 2004), and have further included comparisons between different taxa (e.g. Balakhonov & Rose, 2017). However, comparative studies between taxa may be difficult to interpret, as species-specific skills may not be well represented with a generalised set of tasks (van Horik & Lea, 2017).

Until recently, it was common practice to ignore the variation found between individuals in cognitive tests, extrapolating the abilities of a few exceptional animals to an entire species (Thornton & Lukas, 2012). However, such variation plays a crucial role in understanding how cognitive mechanisms develop and evolve (Boogert et al., 2018), with profound consequences on individuals' fitness (Dingemanse et al., 2002; Thornton & Lukas, 2012). Various dimensions of fitness may be affected by cognitive performance, including reproductive success (blue gourami fish, *Trichogaster trichopterus*: Hollis et al., 1997; japanese quail *Coturnix japonica*: Mahometa & Domjan, 2005); growth rate (grasshopper, *Schistocerca americana*: Dukas & Bernays, 2000); and foraging success (*B. terrestris*: Raine & Chittka, 2008); as well as basic aspects of decision-making such as where and how to find food (Giraldeau, 1984).

Intraspecific variation in cognitive abilities has been extensively studied in humans through the use of psychometric IQ tests that evaluate a "general intelligence" factor termed '*g*' (Shaw & Schmelz, 2017). This factor correlates cognitive abilities in multiple broad domains of cognitive abilities (e.g. memory, processing speed, spatial ability, reasoning: Deary et al., 2010) and predicts that individuals who excel in one cognitive domain will usually do so in others (Amici et al., 2012; Deary et al., 2010). More recently, using batteries of cognitive tests, evidence for *g* has been reported in birds (Shaw et al., 2015), rodents (Galsworthy et al., 2002; Matzel & Han, 2003) and primates (Banerjee et al., 2009; Herrmann & Call, 2012). The existence of *g* in non-human animals however is very much contested, as many argue animals are incapable or having such a general intelligence and instead possess domain-specific abilities (i.e. uncorrelated, independent abilities) (Burkart et al., 2016). Studies with primates, for instance (e.g. Amici et al., 2012), have found no correlation between individuals' different cognitive traits, suggesting cognitive domains that evolved independently for a particular set of socioecological circumstances, resulting in species that have increased cognition in some domains but not others (i.e. 'modular-minds': Amici et al., 2012).

In the rest of this chapter, I begin by describing some of the mechanisms underlying individual variation in cognitive ability, including heritability, the developmental environment and the phenotypic traits and states of animals (Section 2.3). I then go on to detail the relationships between cognitive ability and six phenotypic traits and states reported in a number of studies. Lastly, I discuss in detail some of the issues of testing cognition in captivity and the reliability of generalizing such findings to wild populations (Section 2.4).

2.3 INDIVIDUAL DIFFERENCES IN COGNITION

Despite the importance of individual differences in cognition for fitness, little is known about how such differences may arise. Three non-mutually exclusive hypotheses have been proposed and tested to varying degrees. Individuals within a population could differ in their cognitive abilities because of (1) differences in genotype (Galsworthy et al., 2005; Hopkins & Russell, 2014), (2) differences in developmental trajectory (Kotrschal & Taborsky, 2010) and the environment experienced during their lifetimes (Pravosudov et al., 2005; Roth et al., 2010), and/or (3) the phenotypic traits and states that determine day-to-day behaviour. In the sections below, I provide a brief description of these three possible causes of variation in cognitive abilities

2.3.1 Heritability

If a given cognitive ability has fitness consequences, these traits will be subject to selection (Sorato et al., 2018). As such, variation in cognitive abilities will have evolutionary consequences only when such variation can be transmitted from one generation to another (Dingemanse et al., 2002). While the heritability of cognitive traits has been extensively recorded in humans (e.g. Bartels et al., 2002), research in other animals has been more limited, although evidence for a heritable *g* factor has been reported in primates (*P. troglodytes*: Hopkins & Russell, 2014) and rodents (mice, *Mus* sp: Galsworthy et al., 2005). More recently, Sorato et al. (2018) reported moderate heritability in reversal learning abilities (i.e. the ability to reverse the meaning of cues that had been previously associated) in red junglefowl (*Gallus gallus*). Nevertheless, evidence for heritability in cognitive traits has so far been scarce due to the lack of cognitively-tested individuals of known pedigree (Boogert et al., 2018; Sorato et al., 2018). Moreover, because heritability estimates are influenced by environmental conditions, most studies assessing heritability have been restricted to the laboratory where animals can be bred and tested in standardised conditions.

2.3.2 Developmental Environment

Differences in the quality of the environment, whether physical or social, during ontogeny may result in individual differences in cognitive abilities in later life. On the one hand, a poor physical environment may promote the enhancement of cognitive abilities if survival is dependent on such abilities under these conditions. For example, studies on two populations of black-capped chickadees (*Poecile atricapillus*) have shown that birds who grew-up in harsher conditions outperformed individuals from a more stable environment in both spatial memory and learning tasks (Pravosudov & Clayton, 2002; Roth et al., 2012). On the other hand, the development of cognitive abilities may suffer in poor environments if the body's resources are increasingly diverted towards somatic maintenance. For instance, children of low socioeconomic status often perform poorly in cognitive tests compared to those who have experienced better circumstances during development (Deary et al., 2010). Additionally, differences in individuals' states during early life may result in different cognitive pathways. Boogert et al. (2013) for example, found that both, pre-natal and post-natal stressors in juvenile quails (*Coturnix japanica*) resulted in differences in social learning and foraging abilities in adulthood.

2.3.3 Phenotypic Traits And States

Much of animals' day-to-day behaviour is affected by their phenotypic traits and/or current states. For instance, with respect to sex differences, males may prioritize anti-predator behaviour over foraging, while females prioritize the acquisition of resources to sustain their young (Boinski, 1988; Reader & Laland, 2000). Similarly, with respect to social rank, low-ranking animals may have alternative diets in order to avoid being in closer proximity to, and thus at greater risk of aggression from, dominant conspecifics (Murray et al., 2006).

Differences in behaviour due to phenotypic traits and/or states are likely to determine the sorts of stimuli that individuals experience throughout their lives, possibly promoting or impeding the development of cognitive abilities. One of the difficult aspects of measuring individuals' cognitive abilities in the wild is obtaining a sufficiently large and representative sample with which to quantify variation (especially for social animals, where there are also confounding effects of social learning). Testing animals in captivity potentially overcomes these problems, but may change the animals' inherent behaviours. In the following section, I describe in detail a number of phenotypic traits and states commonly measured in cognitive evaluations as a possible cause of variation in cognitive abilities.

Influence of phenotypic traits and states on cognitive abilities

Evidence from a variety of species indicates that a range of phenotypic traits and state variables may influence individual cognition. Amongst these are: sex, age, social position, behaviour towards novelty, risk assessment behaviour (i.e. vigilance) and stress responses (Table 2.1). It's worth noting that an individual's behaviour may not be determined by a single trait but by a combination of several. For instance, in gregarious species where the individual's social life is governed by its position in the dominance hierarchy, the emotional state of an individual may vary according to its social status. Individuals of low rank, commonly the recipients of aggression and displacements, are more likely to experience acute stressors (Abbott et al., 2003). Castles et al. (1999) for example, reported higher rates of self-directed behaviours, commonly used as indicators of the psychological state of an individual (Maestripieri et al., 1992), in subordinate female olive baboons (*Papio anubis*) whenever a dominant individual was near than when a subordinate was close.

Table 2.1 Overview of studies that have evaluated individual differences in cognitive abilities.

Species (ordered by taxon then alphabetically by common name)	**Reference**	**Setting**	**Task / Behaviour**	**Characteristics Tested**
Carnivores				
Coyote *Canis latrans*	Gilbert-Norton, 2009	Captive	Operant learning task Spatial foraging task	Social Rank
Meerkat *Suricata suricatta*	Thornton & Samson, 2012	Free-ranging	Extractive foraging tasks	Sex Age Social Rank
Spotted hyena *Crocuta crocuta*	Benson-Amram & Holekamp, 2012	Free-ranging	Problem-solving task Innovation	Age Neophobia-neophilia
Ungulates				
Domestic pigs *Sus scrofa*	Held et al., 2000	Captive	Competitive foraging task	Social Rank
Goat *Capra hircus*	Nawroth et al., 2017	Captive	Visual discrimination task	Personality*
Primates				
Bonobos *Pan paniscus*	Boose et al., 2013	Captive	Extractive foraging tasks Tool use	Sex
Capuchin monkey *Cebus apella*	Fragaszy & Visalberghi, 1990	Captive	Extractive foraging tasks Innovation Tool use	Risk assessment behaviour
Capuchin monkey *Cebus apella*	Fragaszy et al., 1994	Captive	Extractive foraging task Task	Age Neophilia
Chacma baboons *Papio ursinus*	Carter et al., 2014	Free-ranging	Hidden-food task Novel food task	Age Neophilia (measured as boldness)
Chimpanzee *Pan troglodytes*	Hopper et al., 2014	Captive	Problem-solving foraging task	Age Sex Personality*

Species **(ordered by taxon then alphabetically by common name)**	**Reference**	**Setting**	**Task / Behaviour**	**Characteristics Tested**
Chimpanzee, *Pan troglodytes*	Lonsdorf, 2005	Free-ranging	Extractive foraging Tool use	Sex
Chimpanzee *Pan troglodytes*	Reader & Laland, 2001	Free-ranging & Captive	Innovation	Sex Age Social Rank
Golded-headed lion tamarin *Leontopithecus chrysomelas* Golden lion tamarin *Leontopithecus rosalia* Black lion tamarin *Leontopithecus chrysopygus* Emperor tamarin *Saguinus imperator* Cotton-top tamarin *Saguinus oedipus* Silvery marmoset *Callithrix argentata* White-headed marmoset *Callithrix geoffroyi*	Kendal et al., 2005	Captive	Extractive foraging tasks Innovation	Age Neophilia
Grey mouse lemurs *Microcebus murinus*	Dal-Pan et al., 2011	Captive	Spatial memory task	Stressors
Long-tailed macaques *Macaca fascicularis*	Bunnell & Perkins, 1980	Captive	Problem solving tasks	Social rank
Long-tailed macaques *Macaca fascicularis*	Toxopeus et al., 2005	Captive	Colour and shape discrimination task	Stressors
Rhesus macaques *Macaca mulatta*	Drea & Wallen, 1999	Captive	Colour discrimination tasks	Social Rank
Ruffed Lemurs *Varecia varegata* & *Varecia rubra*	Dean et al., 2011	Captive	Innovative foraging tasks Social Learning	Sex
Rodents				
Laboratory mice Mus spp.	Barnard & Luo, 2002	Captive	Spatial learning task	Social Rank

Species (ordered by taxon then alphabetically by common name)	Reference	Setting	Task / Behaviour	Characteristics Tested
Laboratory mice Mus sp.	Fitchett et al., 2005	Captive	Spatial memory task	Social Rank Stressors
Rat Rattus sp.	Korol et al., 2004	Captive	Spatial learning task Spontaneous alteration task	Sex Stressors
Rat Rattus sp.	Conrad et al., 2004	Captive	Spatial memory task	Sex Stressors
Rat Rattus ssp.	Shors, 2001	Captive	Instrumental learning tasks	Stressors
Birds				
Arabian babblers *Turdoides squamiceps*	Keynan et al., 2015, 2016	Free-ranging	Problem-solving task Generalisation task	Social Rank
Black-capped chickadee *Poecile atricapillus*	Guillette et al., 2011	Captive	Acoustic discrimination task	Neophilia
Black-capped chickadee *Poecile atricapillus*	Laland & Reader, 1999	Captive	Foraging task Innovation Problem-solving	Sex Neophilia
Carib grackle *Quiscalus lugubris* Lesser Antillean bullfinch *Loxigilla noctis* Shiny cowbird *Molothrus bonariensis* Zenaida dove *Zenaida aurita* Common ground dove *Columbina passerine*	Webster & Lefebvre, 2001	Wild-caught	Extractive foraging task Innovation	Neophobia
Chimango caracara *Milvago chimango*	Biondi et al., 2010	Wild-caught	Problem-solving task Innovation	Age Neophobia-Neophilia
Domestic chick *Gallus gallus domesticus*	Nicol & Pope, 1999	Captive	Operant learning task Social learning	Dominance Rank

Species (ordered by taxon then alphabetically by common name)	**Reference**	**Setting**	**Task / Behaviour**	**Characteristics Tested**
Domestic chick *Gallus gallus domesticus*	Vallortigara, 1996	Captive	Colour and position discrimination task	Sex
European starling *Sturnus vulgaris*	Boogert et al., 2006	Wild-caught	Extractive foraging task	Social Rank Neophobia
Florida scrub-jay *Aphelocoma coerulescens*	Bebus et al., 2016	Free-ranging & wild-caught	Associative learning task Reversal-learning task	Neophobia-Neophilia Stressors
Great tit *Parus major*	Morand-Ferron et al., 2015	Free-ranging & Captive	Associative learning task	Age
Great tit *Parus major*	Titulaer et al., 2012	Wild-caught	Colour and position learning task	Sex Neophilia
Hihi *Notiomystis cincta*	Franks & Thorogood, 2018	Free-ranging	Colour and position learning task	Age
Magpies *Cracticus tibicen dorsalis*	Mirville et al., 2016	Free-ranging	Associative learning task	Age
Ravens *Corvus corax*	Range et al., 2006	Captive	Colour and position discrimination tasks	Sex
Satin bowerbird *Ptilonorhynchus violaceus*	Keagy et al., 2009	Free-ranging	Problem-solving task	Sex Age
Satin bowerbird *Ptilonorhynchus violaceus*	Keagy et al., 2011	Free-ranging	Problem-solving tasks Mimic repertoire task Bower rebuilding task	Sex
Reptiles				
Eastern water skink *Eulamprus quoyii*	Carazo et al., 2014	Wild-caught	Spatial leaning task	Sex Personality*
Fish				
Brooke trout *Salvelinus fontinalis*	White et al., 2017	Captive	Spatial learning task	Personality*

Species (ordered by taxon then alphabetically by common name)	**Reference**	**Setting**	**Task / Behaviour**	**Characteristics Tested**
Guppy *Poecilia reticulata*	Laland & Reader, 1999	Captive	Foraging innovation task	Sex
Guppy *Poecilia reticulata*	Lucon-Xiccato & Bisazza, 2017; Lucon-Xiccato et al., 2016	Captive	Spatial learning task Numerical discrimination task	Sex
Guppy *Poecilia reticulata*	Trompf & Brown, 2014	Wild-caught	Associative learning task Social Learning	Personality*
Blue gourami *Trichogaster trichopterus*	Hollis et al., 2004	Captive	Associative learning (Pavlovian conditioning)	Social Rank
Invertebrates				
Pond snail *Lymnaea stagnalis*	Lukowiak et al., 2010	Captive	Operant learning task	Stressors

Shown are: (*i*) a list of species, in taxonomic order; including the common and latin (in *italics*) name; (*ii*) authors and year of publication; (*iii*) the experimental setting animals were tested in: “free-ranging” refers to wild animals that were rested in their own habitat, “wild caught” refers to wild animals tested in captivity and “captivity” refers to captive animals tested in captivity; (*iv*) task and/or behaviour evaluated; and (*v*) the individual characteristics tested. Studies that reported differences in neophobia or neophilia as “personality” are marked with an asterisk (*).

One of the aims of this thesis is to explain the individual variation in the cognitive abilities of a population based on five phenotypic traits and states. Below, I describe each one of these phenotypic variables and how they have the potential to influence individual differences in cognition.

Sex

Sex-dependent differences in cognition have been recorded in a variety of abilities, including spatial cognition (Gaulin & Fitzgerald, 1986; Yaskin, 2013), innovation (Reader & Laland, 2001), and learning (Titulaer et al., 2012). These differences could reflect ultimate and proximate mechanisms and could largely be attributed to sex-specific characteristics, such as hormones (Luine et al., 2007), mating range (Yaskin, 2013) and personality (Titulaer et al., 2012). For instance, Gaulin and Fitzgerald (1986) reported that male meadow voles (*Microtus pennsylvanicus*) have better spatial abilities than females, possibly due to their tendency to have larger home ranges. In another study on female rats, the fluctuation of hormones throughout the oestrus cycle influenced performance in a memory task (Luine et al., 2007). At the same time, studies have shown that individuals of both sexes have a strong preference for mates with valuable cognitive abilities (Thornton & Lukas, 2012). For example, song complexity, a determinant of mate choice in many bird species, was found to be positively related to male zebra finches' learning ability based on a foraging task (Boogert et al., 2011). Generally, in males, behaviours such as mate choice (Boogert et al., 2011), mate attraction (satin bowerbirds, *Ptilonorhynchus violaceus*: Keagy et al., 2009) and foraging efficiency (zebra finch, *Taeniopygia guttata*: Chantal et al., 2016) can all be related to cognitive performance. Likewise, females, may excel at cognitive abilities, such as problem-solving or innovativeness, that allow them for example, to provision larger numbers of offspring (great tit, *Parus major*: Cole et al., 2012), or to manage trade-offs between mate selection and foraging (*P. major*: Bókony et al., 2017).

Age

Age can affect how individuals approach and solve a task. For instance, Manrique & Call (2015) reported that apes (*P. troglodytes*, *Pan paniscus*, *Pongo abelii*, *Gorilla gorilla*) younger than 7 or above 27 years of age failed at a problem-solving task once the cues with which they were trained were reversed. This study, as well as other research (e.g. spotted hyenas, *Crocuta crocuta*: Benson-Amram & Holekamp, 2012; *P. troglodytes*: Reader & Laland, 2001; meerkats, *Suricata suricatta*: Thornton & Samson, 2012), suggests that age-dependent differences in cognitive abilities may be attributed to individuals' physical development (i.e. morphology), experience, and/or persistence. In the first case, juveniles may not have the necessary neural traits to have developed certain cognitive abilities. Studies with humans and other primates show that the frontal cortical regions of the brain and their associated cognitive abilities do not develop until early adolescence (Bourgeois et al., 1994). For example, juvenile rhesus macaques (*Macaca mulatta*), performed poorly compared to adult conspecifics on a suite of discrimination and reversal tasks dependant on frontal cortical function (Weed et al., 2008). In the second case, it has been suggested that adults may be more successful because they acquire greater experience and/or skills through time (Reader & Laland, 2001). However, this is not always borne out in practice: juveniles who explore novel objects at higher rates have been shown to outperform adult conspecifics (Chimago Caracara, *Milvago chimango*: Biondi et al., 2010; callitrichid monkeys: Kendal et al., 2005), and juvenile Guinea baboons

(*Papio papio*) outperformed adults in a reversal learning task assessing cognitive flexibility (Bonté et al., 2014). Lastly, studies have found that behavioural aspects such as motivation and persistence often decline with age (Barbary macaques, *Macaca sylvanus*: Almeling et al., 2016; great apes: Manrique et al., 2013). Juveniles who are more persistent in cognitive tasks often outperform adults (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012).

Social Rank

It is common for gregarious animals to form dominance hierarchies (Boogert et al., 2006). Within such hierarchies, the social rank of an individual can have a significant effect on its everyday life, with dominant animals tending to have priority of access to food and mates (Abbott et al., 2003), with improved survivorship and reproductive success as a result (Smuts et al., 1987). Evidence from several taxa, including birds (starlings, *Sturnus vulgaris*: Boogert et al., 2006; Arabian babblers, *Turdoides squamiceps*: Keynan et al., 2016; domestic chicks, *Gallus gallus domesticus*: Nicol & Pope, 1999), rodents (mice: Barnard & Luo, 2002), carnivores (coyote, *Canis latrans*: Gilbert-Norton, 2009), and primates (long-tailed macaques, *Macaca fascicularis*: Bunnell et al., 1980; Reader & Laland, 2001) indicates that social position can also influence cognitive abilities. There are two possible patterns. In the first case, dominant animals may show superior task performance, because they have more time to explore tasks by displacing others and monopolizing the task. Dominants have shown better performance than subordinates in both foraging tasks (emperor tamarin, *Sanguinus imperator*: Bicca-Marques & Garber, 2005) and learning tasks (*S. vulgaris*: Boogert et al., 2006), including generalization tasks (*T. squamiceps*: Keynan et al., 2016). In the second case, subordinates may show better task performance, because the restriction to quality resources may lead to a stronger motivation to develop novel behaviours to acquire resources before being displaced by a dominant animal (Kummer & Goodall, 1985; Reader & Laland, 2001). For instance, subordinate long-tailed macaques outperform dominants in a complex learning task (Bunnell et al., 1980). Similarly, whilst dominant pigs (*Sus scrofa*) follow and displace subordinates from food sources, subordinates are more likely to relocate the resource (Held et al., 2000). Subordinates' use of such abilities may nevertheless be determined by social information provided by dominants (i.e. social information strategies), whose behaviour is commonly copied as they are deemed more "successful" by conspecifics (*P. troglodytes*: Kendal et al., 2015; *Gallus gallus domesticus*: Nicol & Pope, 1999).

Response to Novelty

Individuals differ in their reaction to novel situations: some animals avoid novelty, while others are attracted to it. While both responses are often considered opposite ends of the same continuum, they are two distinct behaviours (Greenberg, 2003). Neophobia, defined as the aversion to novel stimuli (Bergman & Kitchen, 2009), usually impedes cognitive performance (Reader, 2003; pigeons, *Columba livia*; zenaida doves, *Zenaida aurita*: Seferta et al., 2001; ravens, *Corvux corax*: Stöwe et al., 2006) as neophobic animals are less likely to fully engage with novel situations (Boogert et al., 2006). Studies with captive birds consistently find that neophobic individuals exhibit lower cognitive performance in tasks involving both novel objects (Biondi et al., 2010; Guido et al., 2017; Seferta et al., 2001; Carib grackle, *Quiscalus lugubris*; Antillean bullfinch, *Loxigilla noctis*; shiny cowbird, *Molothrus bonariensis*; *Z. aurita*; ground dove, *Columbina passerina*: Webster & Lefebvre, 2001) and novel environments (Boogert et al., 2006).

Conversely, neophilia, defined as the attraction of an animal towards novel objects (Bergman & Kitchen, 2009; Greenberg, 2003), is commonly associated with greater innovation and successful problem-solving (Benson-Amram & Holekamp, 2012; Greenberg, 2003; Kendal et al., 2005). A well-known measure of neophilia is exploratory behaviour, as more neophilic individuals usually explore or manipulate objects at higher frequencies than less neophilic individuals (Greenberg, 2003). Exploration, defined as any behaviour that provides individuals with knowledge about their environment (Dingemanse et al., 2002), has been found to vary depending on age (callitrichid monkeys: Kendal et al., 2005), sex (*P. major*: Verbeek et al., 1994) and current social position (*C. corax*: Stöwe et al., 2006), and has been extensively studied in cognition-related situations. Research with birds and primates has reported evidence of a relationship between exploratory behaviour and cognitive performance in tasks involving acoustic discrimination (*P. atricapillus:* Guillette et al., 2009), innovation (callitrichid monkeys: Kendal et al., 2005), and social learning (capuchin monkey, *Cebus apella*: Fragaszy et al., 1994).

Animals' responses to novelty have been closely related to differences in personality (Sih & Del Giudice, 2012). In recent years, personality, defined as a suite of correlated behaviours that persist over time (Carere & Locurto, 2011), has been acknowledged as an important source of variation in animals' cognitive abilities (Boogert et al., 2018). For instance, studies have linked personality with a number of cognitive abilities including problem-solving (*P. roglodytes*: Hopper et al., 2014; *P. major*: Zandberg et al., 2016), associative learning, (*G. gallus domesticus*: de Haas et al., 2017; cavie, *Cavia aperea*: Guenther et al., 2014; goats, *Capra hircus*: Nawroth et al., 2017), and social learning (chacma baboon, *Papio ursinus*: Carter et al., 2014); as well as behaviours that can influence cognition such as, task participation (pheasant, *Phasianus colchicus*: van Horik et al., 2016) and foraging (fallow deer, *Dama dama*: Bergvall et al., 2011; *T. guttata*: David et al., 2011). Personality types are maintained across generations (Dingemanse et al., 2002) through fitness-related trade-offs (Nawroth et al., 2017), which are commonly measured through differences in the exploratory behaviour of animals (Titulaer et al., 2012). Animals who are more exploratory, aggressive and/or take more risks are usually classified as bold; while less exploratory and pacific animals are classified as shy (Sih & Del Giudice, 2012). Speed-accuracy tradeoffs (i.e. fast-slow exploring) may additionally determine how novel information is acquired and later used. Bold and fast-exploring animals take more risks, gaining short-term benefits, while shy and slow-exploring animals sacrifice short-term gains but acquire reliable information safely (Sih & Del Giudice, 2012; Verbeek et al., 1994). For instance, slow-exploring great tits (*P. major*) reduced uncertainty by visiting empty feeders more often than fast-exploring conspecifics (Arvidsson & Matthysen, 2016).

Risk Assessment Behaviour

Vigilance behaviour is often used by individuals as a mechanism either to detect predators or to avoid aggression and food theft (i.e. kleptoparasitism) from other members of their group *(S. vulgaris*: Fernández-Juricic et al., 2005; *C. crocuta*: Pangle & Holekamp, 2010). Vigilance is therefore usually related to predator avoidance and group size in the first case, and social factors such as aggression, neighbour proximity and rank in the second (*P. troglodytes:* Kutsukake, 2007; Treves, 2000; *C. crocuta*: Pangle & Holekamp, 2010). At the same time, individual-level traits such as personality may also influence the intensity of vigilance behaviour (grey kangaroo, *Macropus giganteus*: Edwards et al., 2013). While vigilance allows animals to monitor conspecifics and gather information about their surroundings, it is also a costly behaviour as attention is often diverted from other, important activities (Fernández-Juricic et al., 2005). Thus, it is likely that vigilance impairs cognition-related activities (Boogert et al., 2006; Shettleworth, 2010). For example, subordinate capuchin monkeys who were more vigilant while solving a cognitive task were outperformed by dominant individuals (Fragaszy & Visalberghi, 1990), who in many primate taxa normally spend less time being vigilant towards conspecifics (*P. troglodytes*: Kutsukake, 2007).

2.4. COGNITIVE RESEARCH IN WILD AND CAPTIVE ENVIRONMENTS

Captive research has been fundamental in evaluating and understanding the cognitive abilities of animals, particularly in the case of those species that are impossible to test in a wild setting. Since captive conditions appear to offer an ideal environment in which to study cognition without any geographical, social or physical constraint, research on species' cognition in their natural habitat has historically been limited. However, while some studies in captive settings have successfully integrated relevant aspects of the study species' natural habitat, such as their social environment (e.g. Deipolyi et al., 2001; Fagot & Paleressompoulle, 2009; Gazes et al., 2013; Tanaka, 2001) or have considered using ecologically relevant tasks (e.g. Boose et al., 2013; Samuels et al., 2014; Webster & Lefebvre, 2001), two aspects of cognitive studies in captivity may limit their generalisability to wild conditions: (1) captive rearing and captive bias and (2) validity of methods and testing conditions.

2.4.1 <u>Captive Rearing And Captive Bias</u>

One of the appealing aspects of testing cognition with captive-bred animals is that the environment individuals experience during their ontogeny is known to researchers. However, findings with such test subjects are likely to be influenced by the highly controlled and unnatural conditions that they have experienced (Tomasello & Call, 2011), where the environmental and social aspects of behaviour that occur in natural circumstances, and that influence cognitive processing, are often ignored (Rowe & Healy, 2014). For instance, for some captive tests, animals are removed from their natal group to be raised in isolation (*P. troglodytes*: Menzel et al., 1970; *M. mulatta*: Rommeck et al., 2011; baboon, Rowell, 1967), resulting in long-term consequences. Infant rhesus macaques who were separated from their mothers at an early age, for example, had lower social ranks than those that were kept within their family group (Wooddell et al., 2017). Such rearing will determine the sorts of stimuli that individuals experience throughout their development, and this in turn may influence their cognitive abilities and responses to such stimuli in later life.

Captive animals often have different behaviours than their wild conspecifics. Acquired experience through exposure to human-made objects, or the enforced proximity animals have with conspecifics in captivity, most likely promotes the development and spread of different behaviours between captive and wild animals. This is commonly referred to as captivity bias (Haslam, 2013). For example, several studies have reported greater diversity in tool use in captive animals than their wild counterparts (African elephant, *Loxodonta africana;* Indian elephant, *Elephus maximus*: Chevalier-Skolnikoff & Liska, 1993; Haslam, 2013). In addition, animals in frequent contact with humans are often less neophobic and more willing to explore novel objects (Visalberghi et al., 2003), and as a result often outperform wild conspecifics in problem-solving and innovation tasks (*C. crocuta*: Benson-Amram et al., 2013; *Pongo pygmaeus*: Forss et al., 2015; vervet monkeys, *Chlorocebus aethiops*: van de Waal & Bshary, 2011). Some recent studies have fortunately began addressing both of the issues discussed, by ensuring animals are reared with conspecifics and have infrequent contact with humans (e.g. Whiten et al., 2005).

2.4.2 Validity Of Methods And Testing Conditions

Captive research has often relied on testing animals with complex apparatus or while isolated in test chambers (e.g. Fagot & Paleressompoulle, 2009; Galsworthy et al., 2002; Rollin et al., 1963; Warren & Baron, 1956). While such setups have allowed researchers to successfully investigate complex abilities in a wide range of taxa (e.g Manrique et al., 2013), without the confounding effect of conspecifics' presence, the overall methodology likely impacts task performance, as individuals respond differently to such testing environments; for example, in their motivation to participate (van Horik & Madden, 2016), their stress response to isolation (*P. colchicus*: van Horik & Madden, 2016) or their response to the novelty of a task (rhesus macaque, *M. mulatta*: Johnson, 2000). Even when aspects like motivation or neophobia are controlled by restricting food access prior to testing (e.g. Johnson, 2000; common myna, *Sturnus tristis*: Sol et al., 2012; Titulaer et al., 2012) or habituating animals to a testing paradigm (cichlid, *Neolamprologus pulcher*: Bannier et al., 2017; van Horik et al., 2016), this rarely guarantees a 'natural' response.

Many captive tests additionally require the presence of a human demonstrator, particularly in the case of primates, (e.g. *P. troglodytes*: Asano et al., 1982; Herrmann et al., 2007; Schmitt et al., 2012; Vonk & Povinelli, 2011) and/or the training of animals for long periods of time to perform in a given task (e.g. Chantal et al., 2016; de Haas et al., 2017; great apes: Kanngiesser & Call, 2010; *C. apella*: Lakshminarayanan & Santos, 2009; degus, *Octodon degus*: Okanoya et al., 2008; *P. troglodytes*: Tanaka, 2001). While such methods allow researchers to quantify individuals' performance evenly and accurately, they may obscure the adaptive significance of any cognitive processes that might occur naturally. For example, among caviomorph rodents, Okanoya et al. (2008) demonstrated that degus are capable of tool use, but only after a training period of 2,500 trials. Perhaps unsurprisingly, untrained individuals usually have a low success rate when tested with cognitive tasks (Chalmeau & Gallo, 1993).

2.4.3 Current and future research

Fortunately, research on cognition in wild populations has slowly been expanding to include a wider variety of study species (*L. africana, E. maximus*: Chevalier-Skolnikoff & Liska, 1993; *P. pygmaeus*: Forss et al., 2015; *Corvus frugilegus*: Greggor et al., 2016; kea, *Nestor notabilis:* Huber & Gajdon, 2006; *Tursiops sp*: Krützen et al., 2005; Smolker et al., 2010; *P. anubis*: Laidre, 2008; *Cracticus tibicen dorsalis:* Mirville et al., 2016; *C. aethiops*: van de Waal et al., 2013a; van de Waal et al., 2013b). However, few of these studies focus on individual cognitive abilities (*C. crocuta:* Benson-Amram & Holekamp, 2012; *P. ursinus*: Carter et al., 2014; *P. major*: Cole et al., 2011; hihi, *Notiomystis cincta*: Franks & Thorogood, 2018; *S. suricatta*: Thornton & Samson, 2012). This partly reflects the fact that testing animals in the wild is challenging, leading to small sample sizes that limit the analysis of individual variation. The latter has partly been addressed with the recent inclusion of automated devices in testing (e.g. *P. major*: Morand-Ferron et al., 2015), yet this has so far only been applicable in studies with wild birds or captive mammals (*P. papio*: Fagot & Bonté, 2010). The importance of testing variation under animals' natural conditions cannot be understated if we aim to understand how cognitive abilities develop and evolve in a given environment. This is important not only from the perspective of fundamental science but also if we are to better understand how animals cope with changing environments.

Chapter 3

Study System And General Methods

3.1 INTRODUCTION

Understanding individual differences in cognitive abilities is important because such processes underpin many of the day-to-day behavioural decisions that determine animal fitness (See Chapter 2 for more details). Research on cognition has historically favoured studies on primate species to investigate the evolution of human cognitive abilities (e.g. Amici et al., 2010; Seed & Tomasello, 2010; Tomasello & Call, 1997). As our closest relatives, great apes are amongst most studied (i.e. Herrmann & Call, 2012; Vonk & Povinelli, 2011; Whiten & van Schaik, 2007); however, there is evidence of similar underlying cognitive processes shared across several primate taxa, including humans, apes and monkeys (Reader et al., 2011). From the broader perspective of behaviour and ecology, baboons are amongst the most well-studied primates, partly reflecting their ease of study as approachable, semi-terrestrial primates living in open habitats, and partly reflecting their potential utility as a window into human evolution, as they evolved in parallel to hominins in similar African savannahs (Zinner et al., 2013). As such, chacma baboons, one of the best studied of all baboon taxa, is an ideal species in which to study individual differences in cognition. Here, I provide a general background to chacma baboons, including the baboon population under study; as well as a brief description of the environment in which all field work was carried out. Lastly, I give an overview of the observational and experimental data collection employed in my thesis.

3.2 STUDY SYSTEM

3.2.1 Study Species

Chacma baboons (*Papio ursinus*) belong to the *Cercopithecoidea,* one of the largest primate super-families, more commonly known as the Old World monkeys. The extant members of the *Cercopithecoidea* form the family *Cercopithecidea,* which diverged from other primate lineages approximately 30 million years ago (Raaum et al., 2005; Swindler, 2002). Cercopithecids can be divided into two very distinct groups: Colobines and Cercopithecines (Swindler, 2002). Both subfamilies share distinct morphological features such as marked sexual dimorphism (Page et al., 1999); however, unlike colobines which are almost exclusively arboreal and whose diet consists primarily of leaves, cercopithecines are terrestrial and omnivorous (Page et al., 1999; Swindler, 2002). Taxa in this group, which include macaques, mandrills and baboons, share common characteristics, such as having ischial callosities (coarse patches of skin located above the pelvic bones on which they sit), cheek pouches (Page et al., 1999), and strict social hierarchies (Di Fiore & Rendall, 1994).

Baboons, which form part of the genus *Papio,* are a widely distributed and highly successful species, found in numerous habitats throughout sub-Saharan Africa (Newman et al., 2004; Stone et al., 2012). Like many Old World monkeys, chacma baboons are characterised by multimale-multifemale groups, ranging in size from 13-100 animals (Bulger & Hamilton, 1987; Cheney & Seyfarth, 2007). Infant baboons are born after six months of gestation. Females give birth to a single infant, which remains dependent for approximately one year and is fully independent at roughly 15 months of age (Cheney & Seyfarth, 2007). Females are philopatric, staying throughout their lives in their natal group, where matrilines of related females and their juvenile offspring maintain close social bonds (Silk et al., 2009, 2010). Generally, females become adult at 4-6 years of age. During their oestrus cycles, females develop a sexual swelling around their perineum which acts as a fertility signal (Huchard et al., 2009). In contrast, males become adult at around 9 years of age, after which they usually leave their natal troop and migrate into new troops (Cheney & Seyfarth, 2007). Female baboons can live up to 25-27 years in the wild, while males, who have a higher rate of mortality, can live up to 20 years (Altmann & Alberts, 2003).

Interactions within a baboon troop are characterized by a strict linear dominance hierarchy. In the case of females, dominance ranks are linear and stable. Females inherit their ranks from their mother in inverse relation to their age, with the youngest daughter ranking higher than her older sisters (Engh et al., 2006). High-ranking females largely maintain their status through the support of their kin and other members of the troop, who may offer coalitionary support in aggressive interactions (Silk, 2002). Social status is also reflected in affiliative interactions, especially grooming, which dominant females receive from their kin and lower-ranking conspecifics (Schino, 2001). However, while high-ranking females have priority-of-access to resources and can start to reproduce at an earlier age, low-ranking females can still raise offspring successfully, and often have close social bonds with females from the dominant matrilines (Cheney & Seyfarth, 2007).

Adult males, who are significantly larger than females, out-rank all females and juvenile males. Males form a linear hierarchy that can vary through time based on the outcome of aggressive interactions (Cheney & Seyfarth, 2007). Male rank in the hierarchy is correlated with reproductive success. In this case, physical fights are relatively rare.

Instead, males are involved in competitive displays that act as a signal of male strength and condition (Fischer et al., 2004; Silk, 2002). While adult males rarely develop social bonds with other adult males, they may form friendships with lactating females (with whom they have normally fathered the infant). This provides protection to their offspring, who may be at risk of infanticide from new immigrant males (Cheney & Seyfarth, 2007). See Fig 3.1 for images of chacma baboons at Tsaobis.

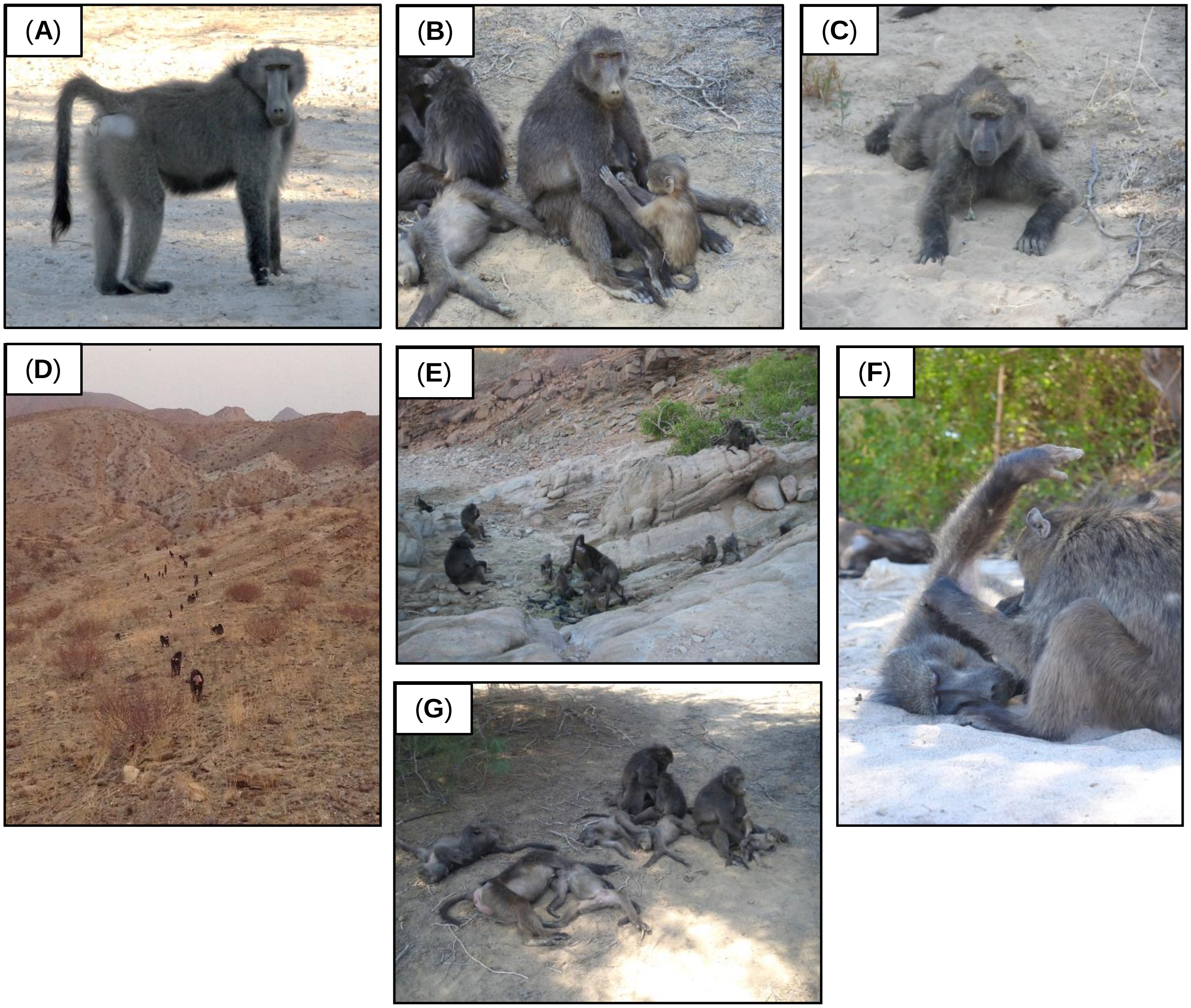

Figure 3.1 Chacma baboons at Tsaobis. (**A**) a grown adult male; (**B**) an adult female and her dependent infant; (**C**) a female juvenile resting. (**D**) a troop returning to their sleeping site at dusk; (**E**) a small group waiting for their turn to drink; (**F**) grooming interaction between a juvenile male and his mother; (**G**) a group of related individuals resting at midday. Photo credits: (A, B, C, D, E & G) C.M.; (F) Zoe Tarren.

3.2.2 Study Site

Tsaobis Nature Park (15° 45’E, 22° 23’S) is dominated by mountains that are fringed by steep foothills and rolling plains. To the north, it is bordered by the ephemeral Swakop

River. The park has a total area of 45,000 ha and an altitude of 683-1445 m (Cowlishaw & Davies, 1997). Rainfall is temporally variable, with a mean of 122.5 mm per year (n = 32 years). Typically, the rainy season occurs between the months of January and April, with no rainfall is recorded between June and August. Temperatures often exceed 40 °C in the shade during the austral summer and can fall as low as 0 °C during winter. The Swakop river supports a diverse plant community, which includes patches of riparian woodland dominated by *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (Cowlishaw & Davies, 1997). The hills around the Swakop riverbed are dominated by perennial grasses and small shrubs and trees, most commonly *Commiphora virgata*. During and following the wet summer months, the baboons will feed on the small invertebrates and vegetation found in the hills; but as the dry austral winter progresses, they increasingly forage on the flowers and pods found in the woodland along the Swakop river (Cowlishaw, 1997) (Fig 3.2).

The study period was characterised by two particularly dry years. To demonstrate that here, the normalized difference vegetation index (NDVI; Pettorelli, 2013), a satellite-based vegetation index which provides a record of environmental quality based on net primary productivity (measured by the light reflected by green vegetation or “greenness”), was used to estimate food availability for the home ranges of the study troops in the two study years. NDVI data over the years 2004-2018 was downloaded from the NASA Earth Observation data website (https://search.earthdata.nasa.gov/search), at 250 x 250 m spatial resolution each separated by a 16 day period (MOTIS 13Q1 v006: Didan, 2015). Home range was estimated using GPS coordinate points taken every 30 min by observers (n = 61662 points, See General Data Collection section below), using kernel density estimates (KDE) to compute 100% isopleth home ranges with the adehabitatHR package (Calenge, 2015). A 1 km extension was added to the estimated ranging area to encompass all possible ranging locations. NDVI estimates from the time during which my fieldwork was conducted indicate low food availability (mean NDVI scores: 2015: 1,253; 2016: 1,044) in comparison with the previous and preceeding years (2014: 1,452; 2017: 1,425). These data were extracted and analysed by PhD student Cassandra Raby. She is a collaborator on my project and made these data available to me.

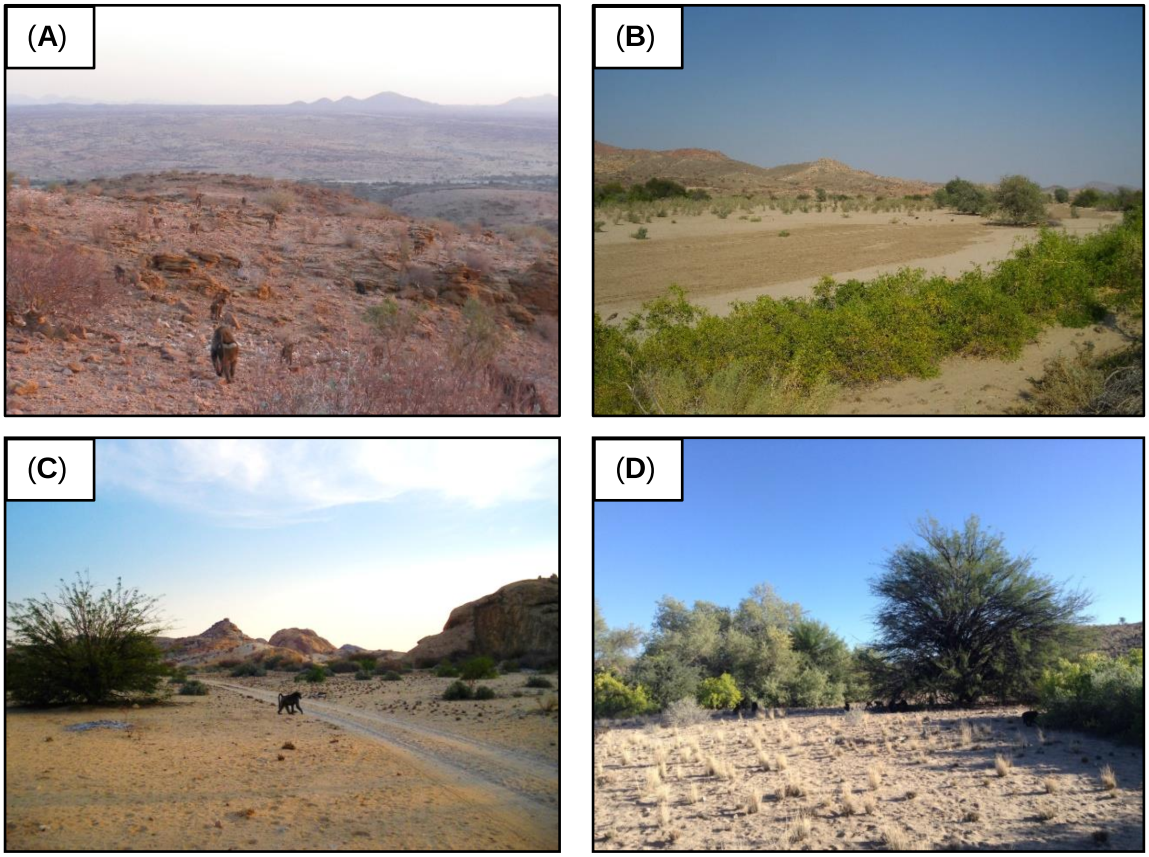

Figure 3.2 Tsaobis Nature Park. (**A**) baboons descending from a rocky hill; (**B**) the Swakop riverbed with patches of riparian woodland; (**C**) a single baboon crossing a man-made road on the plains between foothills; (**D**) baboons foraging on patches of riparian woodland. Photo credits: (A-D) C.M.

3.2.3 Study Population

The Tsaobis Baboon Project focuses on two fully habituated troops of chacma baboons at the Tsaobis Nature Park (Fig 3.3). This individual-based, long-term field study is now in its 19th year, and therefore has detailed contextual and life history information for all the baboons in the study troops. I carried out my fieldwork over a two-month pilot study (November 2014 - January 2015) and two 5-6 months field seasons (April - September

2015; May - September 2016). During this period, the two study groups, L and J, ranged in size from 52 to 68 animals. J troop contained 68 baboons in 2015 and, following a troop split between the 2015 and 2016 field season, 52 animals remained in 2016. The other part of the troop formed a smaller subtroop (M Troop, not included here). See Table 3.1 for troop demographics. All baboons over 4 years of age were individually identifiable through ear notches (Fig. 3.4).

Figure 3.3 Maps indicating the location of the study site. (**A**) map of Southern Africa indicating Namibia in red; (**B**) map of central Namibia indicating the location of the study site marked as “ZSL Tsaobis Baboon Project”.

Table 3.1 Demographic data for J and L troops for 2015-2016.

Year	Troop		Adult	Juvenile	Total
2015	J	Male	7	24	31
		Female	18	19	37
		Total	**25**	**43**	**68**
	L	Male	5	25	30
		Female	18	7	25
		Total	**23**	**32**	**55**
2016	J	Male	5	23	28
		Female	15	9	24
		Total	**20**	**32**	**52**
	L	Male	5	28	33
		Female	18	12	30
		Total	**23**	**40**	**63**

Shown is the total number of baboons in each age and sex category in each troop for each year. The total number for each category is marked in **bold**.

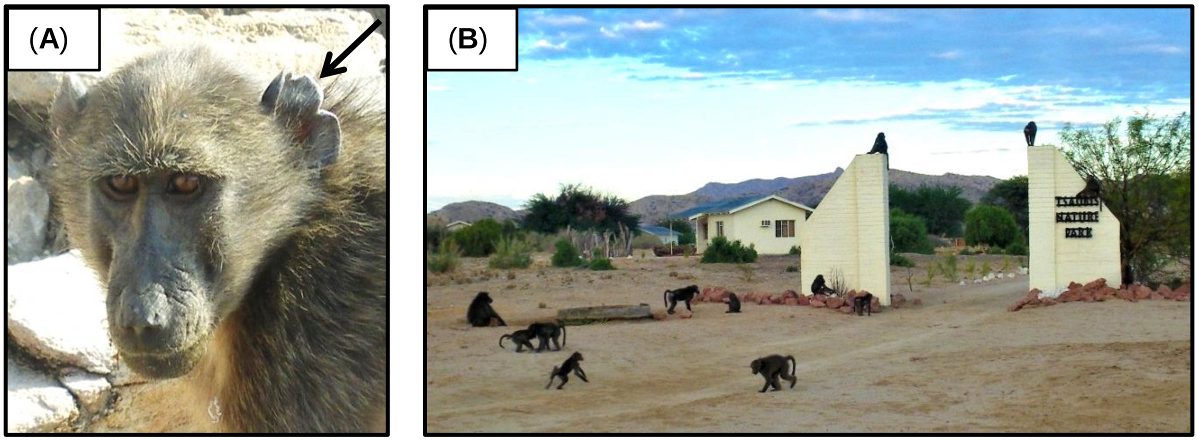

Figure 3.4 Images of the Tsaobis baboons. (**A**) example of a notched juvenile, a black arrow points to the notches on the left ear (top, middle and bottom, although the latter is not visible in this picture); (**B**) baboons play around the entrance of the rest camp. Photo credits: (A-B) C.M

3.3. DATA COLLECTION

3.3.1 <u>Observational Data Collection</u>

Both groups of baboons were observed daily by observers (myself and my field assistants) working on foot from dawn to dusk. Observers used the freely available software Cybertracker (www.cybertracker.org) on individual smart phones (Samsung Galaxy S4, Samsung, Seoul, South Korea) to record dominance and social interactions *ad libitum* and perform focal observations. Baseline data for the wider long-term project involving scan samples and GPS coordinates (Garmin Dakota 20, Garmin Ltd) were additionally collected throughout the day.

Focal observations were conducted throughout both field seasons (2015-2016), each recording all affiliative and aggressive interactions and the activities of the focal individual, including its foraging behaviour (Fig 3.5). Appendix S1, Table S1.1 describes the ethogram used for the focal observations. During the focal observations, any behaviour defined as a “General Activity” in the ethogram, was recorded continuously until the individual switched to another “General Activity” behaviour. All other behaviours (e.g. aggressive & affiliative behaviours) were recorded as events that occurred whilst conducting a “General Activity” and were recorded whenever they were observed. Observations lasted between 20 and 30 min (any observation less than 20 min was discarded) and were distributed evenly across the day over four time periods (0600-0900, 0900-1200, 1200-1500, 1500-1800 h) in each month of study. On any given day, an individual was focal followed no more than once. I collected focal observations both on those animals that participated in the cognitive tasks and those that did not. All individuals were sampled to allow maximum flexibility for tests subjects. Participants were randomly selected from the group according to their sex, age and social status to obtain a representative sample. The test participants who received focals comprised 37 individuals in 2015, 12 individuals in 2016, and a further 15 individuals who were focalled in both years (64 individuals in total). The untested focal animals comprised 46 individuals in 2015 and 36 individuals in 2016, of whom 28 were sampled in both years. The number of focal observations each individual received varied according to year and whether they were task participants (Table 3.2 A, B).

Those animals tested in 2015 (n = 38) were observed for a maximum of 1 h across two 30-min focal observations in each of the time periods, generating on average 3.5 h per focal individual per month (range 1.5 – 4.0) and a total average (median) of 14 h of focal observations per individual. Those remaining individuals that were not tested but still followed in each time period (n = 46), were observed for a maximum of 30 min in each time period, generating on average 1.9 h per focal individual per month (range 0.5 – 2.0) and a total average (median) of 7.5 h of focal observations per individual. Due to logistical constraints, I was unable to conduct focal observations for the month of June in either troop.

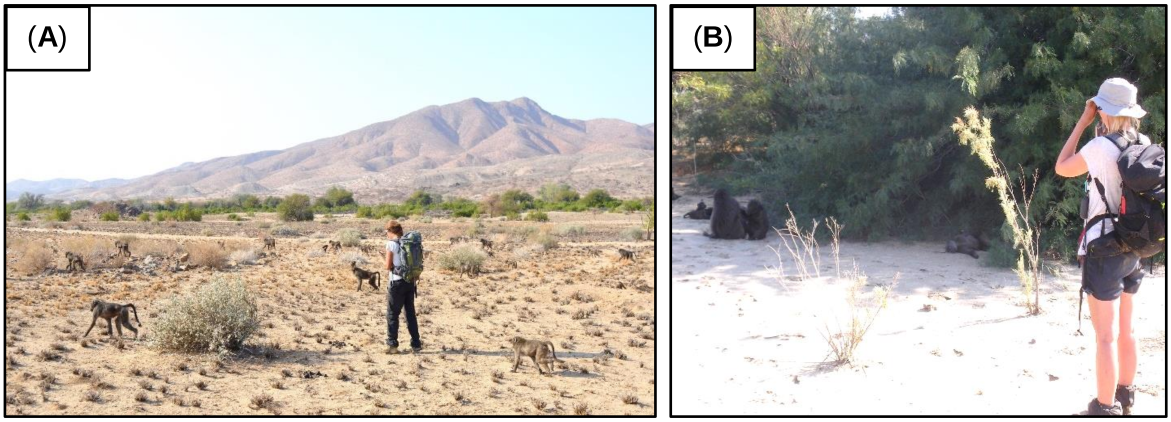

Figure 3.5 Every-day routine during the field season. (**A**) the author (C.M.) follows one of the troops under study early in the morning; (**B**) an observer stands at a distance while identifying the baboons involved in a grooming interaction. Photo credits: (A) Zoe Tarren; (B) C.M.

In the following field season, those individuals that were tested in both the 2015 and 2016 field seasons (n = 15) were observed for a maximum of 1 h across two 30 min focal observations in each of the time periods, generating on average 3.5 h of observation per focal individual per month (range 1.5 - 4) and a total average (median) of 12.5 h. Baboons tested in 2016 only (n = 12) and those untested (n = 36) were observed for a maximum of 30 min in each time period in every month of study (with the exception of 3 animals in the former group, which could not be observed for the month on June), generating on average 2.1 h and 2.5 h per focal individual per month (range 0.5-4 h in both cases) for each group, respectively. In total, each baboon tested was observed on average (median) for 5.3 h and 8.7 h per month for individuals tested and untested in 2016, respectively. Differences in the observation time of animals per month was due to differences in the time following each troop during this field season.

Table 3.2 Average number of hours of focal observations for tested and untested individuals in each troop in the (**A**) 2015 field season; (**B**) 2016 field season.

(**A**)

Month	Tested		Untested	
	J	L	J	L
May	1.9	2.0	1.7	1.8
June	N/A	N/A	N/A	N/A
July	4.0	4.0	1.7	1.8
August	4.0	4.0	2.0	1.9
September	4.0	4.0	2.0	2.0
Total Average	**14.0**	**14.0**	**7.4**	**7.5**

(**B**)

Month	Tested in 2015 & 2016		Tested in 2016 only		Untested	
	J	L	J	L	J	L
June	N/A	3.5	N/A	N/A	N/A	3.6
July	4.0	3.3	3.0	1.8	2.0	2.4
August	4.0	4.0	2.0	1.9	2.0	2.0
September	2.2	4.0	2.0	N/A	1.5	4.0
Total Average	**10.2**	**14.8**	**7.0**	**3.7**	**5.5**	**12.0**

Shown is the average number of hours each individual was tested according to the month of the year, troop and test status (tested/ untested). The total average of focal observation hours for each troop in each month is shown in **bold.**

3.3.2 Experimental Data Collection

Three cognitive tasks were carried out with the Tsaobis baboons during the 2015-2016 field seasons. All three tasks were designed to test the associative learning abilities of individuals. I focused on associative learning because it is a widespread, highly conserved process (Ginsburg & Jablonka, 2010) that determines a number of behaviours linked to fitness and as such, is subject to selection (Morand-Ferron, 2017).

I began with an associative learning task based on operant conditioning. Operant conditioning involves the reinforcement of an association by one's own behaviour (Pritchett & Mulder, 2004). The task involved the presentation of two piles of coloured corn kernels (i.e. green and red), one of which was made unpalatable with a bitter solution (Fig 3.6A). The animals were tested to see if they could learn the association between the colour and palatability of the kernels. I then presented a second associative learning task, also based on operant conditioning that involved the presentation of two paper bags using the same colour cues as the previous task, in which the colour of the bag indicated the presence of a reward inside (Fig 3.6B). The animals were tested to see if they could learn the association between the colour of the bag and its contents. This second task was also designed to have the flexibility to act as a generalisation task following the potential learning of the colour-reward association in the preceding task, although the outcome of that task precluded this approach (see Chapter 4). My final associative learning task was a second-order conditioning task, based on Pavlovian conditioning. In Pavlovian conditioning, a behaviour is modified by the association between two stimuli which are presented consecutively (Pavlov, 1927). This task consisted of a series of associations that included the pairing of a clicker and food, a clicker and a neutral stimulus (i.e. a blue cardboard square) and a neutral stimulus on its own (Fig 3.6C). The animals were tested to see if they could learn an association between the neutral stimulus and a reward (food) via another stimulus, the clicker.

A summary of the number of individuals tested and the average number of trials per task can be found in Table 3.3; while Table 3.4 provides a summary of the tasks presented to each individual. All trials in each experiment were conducted following the same procedures as those previously used in this population for personality assessment experiments involving individual novel food presentations (Carter et al., 2014), i.e. the tasks were presented to each baboon alone and out of sight of conspecifics. In the first and second experiments, each trial was conducted between 0600 and 1000 to control for possible differences in satiation through the day. In the third experiment, tasks were first presented at 0700 and continued through the day at one-hour intervals. All trials were filmed (Canon Vixia HF R300) to facilitate data extraction. For further details on all three experiments see the respective chapters (Chapters 4, 5 & 6). Task protocols were assessed and approved by the Ethics Committee of the Zoological Society of London (BPE 727). All research was approved by the Ministry of Environment and Tourism in Namibia (Research Permits 2009/2015). Individuals were not separated from their group or forced to interact with any task, as participation was voluntary. During testing, no animals were injured and any risk of physical danger (i.e. aggression from conspecifics) associated with task participation was minimized by presenting each individual with the task whilst out of sight from conspecifics. Food items used in each task were familiar to this population, having been presented to them in previous experiments (Lee & Cowlishaw, 2017).

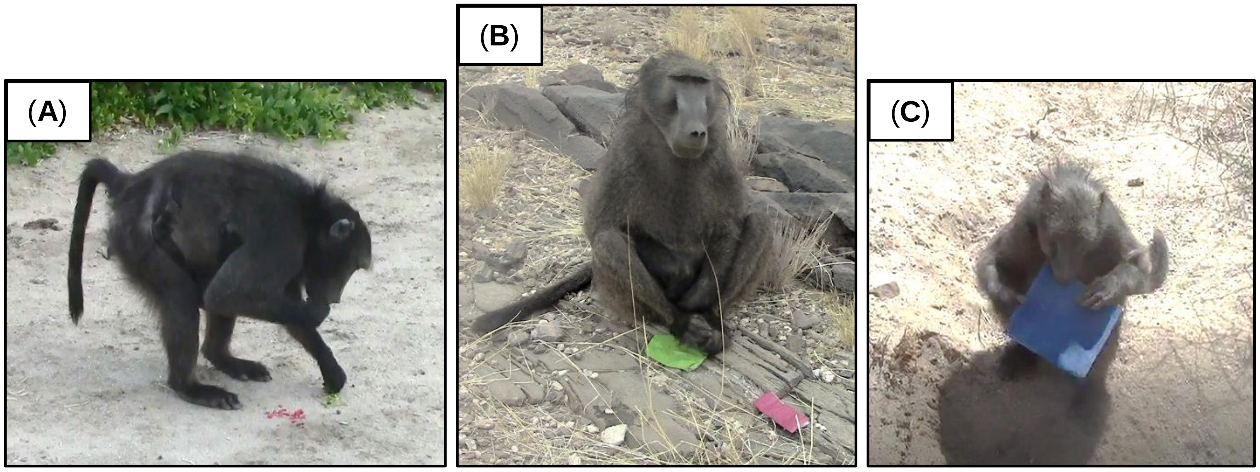

Figure 3.6 Study subjects participating in each task. (**A**) adult female LF04 being tested with the associative learning task involving coloured corn kernels; (**B**) adult male JM64 being tested with the associative learning task involving coloured paper bags; (**C**) adult female JF40 tested in the second-order-conditioning task handling a neutral stimulus. Photo credits: (A-C) C.M.

Table 3.3 Summary of experiments

Experiment	Number of trials	Troop	Male		Female		Total individuals
			A	Jv	A	Jv	
Associative Learning (Corn Kernels)	162 trials; x̅: 4.3	J	4 (**57**)	7 (**50**)	8 (**44**)	3 (**60**)	38 (**43**)
		L	2 (**40**)	7 (**37**)	7 (**39**)	1 (**100**)	
Associative Learning (Paper Bags)	111 trials; x̅: 3	J	3 (**43**)	7 (**50**)	8 (**44**)	3 (**60**)	37 (**42**)
		L	2 (40)	7 (**37**)	7 (**39**)	1 (**100**)	
Associative Learning (Second-Order Conditioning)	243 trials; x̅: 9	J	0 (**0**)	1 (**11**)	2 (**13**)	0 (**0**)	27 (**40**)
		L	3 (**75**)	9 (**56**)	11 (**65**)	1 (**100**)	

Shown are the number of trials per experiment and mean number of trials per individual (x̅) and the demographic data of baboons tested according to sex (Males, Females), age (A, adults; Jv, juveniles) and troop (J, L). In **bold**, in parentheses, the percentage (%) of the population the study sample represents.

Table 3.4 Summary of tasks presented to each study subject

Individual ID	Sex	Age	Troop	Associative Learning (Corn Kernels)	Associative Learning (Paper Bags)	Associative Learning (Second-Order Conditioning)
UJM12	M	A	J	✓	✓	
JM64	M	A	J	✓	✓	
UJM21	M	A	J	✓	✓	
JM42	M	J	J	✓	✓	
JM50	M	J	J	✓	✓	
JM52	M	J	J	✓	✓	
JM45	M	J	J	✓	✓	
JM44	M	J	J	✓	✓	
JM39	M	J	J			✓
JM40	M	J	J	✓	✓	
JM46	M	J	J	✓	✓	
JF44	F	A	J	✓	✓	
JF07	F	A	J	✓	✓	
JF08	F	A	J	✓	✓	
JF03	F	A	J	✓	✓	✓
JF36	F	A	J	✓	✓	
JF37	F	A	J	✓	✓	
JF28	F	A	J	✓	✓	
JF38	F	J	J	✓	✓	
JF39	F	J	J	✓	✓	
JF40	F	J	J	✓	✓	✓
JM17	M	A	L			✓
LM34	M	A	L	✓	✓	✓
JM28	M	A	L	✓	✓	
JM08	M	A	L			✓
LM15	M	J	L	✓	✓	✓
LM18	M	J	L			✓
LM20	M	J	L	✓	✓	✓
LM26	M	J	L	✓	✓	✓
LM27	M	J	L			✓
LM28	M	J	L	✓	✓	✓

Individual ID	Sex	Age	Troop	Associative Learning (Corn Kernels)	Associative Learning (Paper Bags)	Associative Learning (Second-Order Conditioning)
LM31	M	J	L	✓	✓	✓
LM23	M	J	L			✓
LM24	M	J	L	✓	✓	
LM30	M	J	L	✓	✓	
LF03	F	A	L	✓	✓	✓
LF04	F	A	L			✓
LF14	F	A	L	✓	✓	✓
LF17	F	A	L			✓
LF20	F	A	L	✓	✓	✓
LF16	F	A	L			✓
LF18	F	A	L	✓	✓	
LF19	F	A	L	✓	✓	✓
LF27	F	A	L	✓	✓	✓
LF22	F	A	L			✓
LF23	F	A	L			✓
LF28	F	A	L	✓	✓	✓
LF29	F	J	L	✓	✓	✓

Shown are the individual IDs of each participant, their sex, age class and troop membership. A tick mark (✓) indicates the task individuals were evaluated with.

3.4. CORE HYPOTHESES

In this thesis, I aim to: (1) to investigate individual differences in the cognitive abilities of animals using the three tasks presented in the field; (2) to determine whether and which individual traits may influence these abilities; and (3) to explore some of the issues that might explain differences in cognitive performance between captive and wild settings. To explore what may underlie individual differences, I used a common set of five hypotheses that relate differences in cognitive performance to differences in phenotype and state, namely, individuals' sex, age, social rank, response to novelty (from here on referred to as "personality") and risk assessment behaviour. The previous chapter (Chapter 2) introduced the potential effects of each of these phenotypic traits/states on cognitive ability in the context of the wider literature. Their application in my study system, and the specific hypotheses/predictions I tested, are detailed in Table 3.4. Not all hypotheses will be tested in every chapter: hypotheses 1-5 are tested in the two of the three associative learning experiments (Chapters 4 & 5). In the third associative learning experiment (Chapter 6) I was unable to test these hypotheses the sample sizes were sufficient to assess learning but not to explore the individual correlates of such learning. These core hypotheses only relate to learning performance in the first three experiments; however, I explored similar hypotheses involving the same phenotypic traits/states in Chapters 7 & 8. The relevant hypotheses and predictions are specified in those chapters. Across individuals, I classified sex, rank, and personality as phenotypic traits, as the associated characteristics of each trait persist throughout individuals' life; and age and risk assessment behaviour as states, as the associated characteristics are state-dependent and may only occur during specific periods of an individuals' lifetime. In order to quantify these five measures of individual trait/state, I adopted the following approach:

(1) Sex (female/male) was assigned by physical appearance in baboons, which are sexually dimorphic (e.g. body size, primary sexual characters). Sex was additionally determined by the shape of the ischial callosities. Males possess a continuous, long callosity that stretches across the gluteal region; while females possess two tear drop-shaped callosities on opposite sides of their gluteal area to accommodate the growth of their sexual swelling.

(2) Age class (adult/juvenile) was defined by menarche and canine development in females and males, respectively. Prior to their first menstrual bleeding, females were considered juveniles, after which they are considered adults. Likewise, males were considered juveniles prior to the development of secondary-sexual characters: long canines, the appearance of canine ridges, large testes and large size (Altmann et al., 1981).

(3) Dominance rank was determined from dominance interactions recorded *ad libitum* using Cybertracker software (www.cybertracker.org) on smart phones (Samsung Galaxy S4, Samsung, Seoul, South Korea). All displacements, supplants, attacks, chases and threats between two individuals, along with the direction of interaction, were recorded. The troops' dominance hierarchies were calculated separately for each year using Matman (Noldus Information Technology) and standardized from 0 to 1 to control for troop size. Data form both years confirm a strongly linear hierarchy (2015: Landau's corrected linearity index $h'_{J\ TROOP} = 0.343$, $h'_{L\ TROOP} = 0.412$, $n_J = 946$, $n_L = 861$; 2016: $h'_{J\ TROOP} = 0.156$, $h'_{L\ TROOP} = 0.202$, $n_J = 1081$, $n_L = 1326$; $p < 0.001$ in all cases).

(4) Personality was assayed by boldness, using an established experimental approach in which individuals' responses to a novel food (an eighth of an apple dyed blue in 2015

and three popped corn kernels in 2016) were assessed. An individual's boldness was defined as the time spent inspecting the item. This measure was estimated once during each year of study (2015-2016), but was previously found to be highly repeatable over three years (r = 0.26, P = 0.02: Carter et al., 2012). These experiments were carried out by Dr Alecia Carter in 2015 and 2016 as part of her long-term study of individual variation in boldness (for further detail see: Carter et al., 2012; Carter et al., 2014). Dr Carter is a collaborator on my project, and she made these experimental data available to me.

(5) Risk assessment behaviour was defined as the number of times an individual lifted its head to scan its surroundings during the experimental trials, and expressed as a rate per trial (the number of vigilance events observed divided by the total time of the trial (s)).

Table 3.5 Core hypotheses and predictions

Trait	Hypotheses and justification
1. Sex	Female baboons will be more successful in a given task. This hypothesis is based on two reasons. First, because females are philopatric while males disperse (See “Study Species”), females might have better associative learning skills because they have more opportunity to benefit from learnt associations involving local resources than males. Second, during gestation and lactation, females need to increase dietary energy consumption while they are especially sensitive to plant secondary compounds (Key & Ross, 1999; Sherman & Flaxman, 2002), which might select for better associative learning abilities.
2. Age	Adult baboons will outperform juveniles. Although juvenile chacma baboons have higher levels of inquisitiveness (i.e. exploratory behaviour) than their older conspecifics (Bergman & Kitchen, 2009; Carter et al., 2014), I might expect any associated advantage in cognitive testing to disappear once this tendency has been controlled for statistically (through individual personality using boldness, see hypothesis 4 below). As a result, I would expect adults to outperform juveniles because of their greater experience in associative learning.
3. Social Rank	There are two possible predictions. First, that dominants will outperform subordinates, for two reasons: because (1) they could have greater access to key resources (such as more nutritional foods in early life) that allow for better development and maintenance of cognitive abilities; and/or (2) they are unlikely to be displaced and consequently can afford more time to assess a cognition-related situation (Barton & Whiten, 1993; Shopland, 1987). Second, that subordinates will outperform dominants because their low social status commonly restricts their opportunity to forage in high quality food patches (Lee et al., 2016). As such, subordinates may be more motivated to explore novelty. For instance, subordinate baboons may run ahead of dominant animals to access resources before the dominant arrives (Brain, 1990).

4. Personality	Bolder, more exploratory baboons will outperform their shyer, less exploratory conspecifics. Previous research on this population (Carter et al., 2014) has demonstrated that these baboons consistently differ in their exploration (i.e. neophilia) of novel food items (with respect to their response to a novel food presentation). I will test whether such variation affects learning ability, on the basis that bolder animals are likely to have higher rates of interaction with a novel task and therefore more opportunity to learn.
5. Risk Assessment	Those baboons who are more vigilant while solving a task will be outperformed by their less vigilant conspecifics. Baboons that perceive a high risk of aggression from conspecifics (i.e. due to social rank) and/or attack by predators (I.e. due to age differences) are likely to be more vigilant (social monitoring: Alberts, 1994; predator detection: Cowlishaw, 1998). However, once the effects of social rank and age which mediate risk assessment are controlled for, I would expect vigilant behaviour to interrupt task solving and lead to poorer task performance.

Shown are the five core hypotheses applied to the Tsaobis baboon study system and their related predictions about how trait and state might affect cognitive performance in three associative learning tasks.

Chapter 4

Exploring Individual Variation In Associative Learning Abilities Through An Operant Conditioning Task In Wild Baboons

An earlier version of this chapter was submitted to the journal PLoS ONE and invited for resubmission. Currently the manuscript is under revision by the authors.

4.1 ABSTRACT

Cognitive abilities underpin many of the behavioural decisions of animals. However, we still have very little understanding of how and why cognitive abilities vary between individuals of the same species in wild populations. In this study, I assessed the associative learning abilities of wild chacma baboons (*Papio ursinus*) across two troops in Namibia with a simple operant conditioning task. I evaluated the ability of individuals to correctly associate a particular colour of corn kernels with a distasteful flavour through repeated presentations of two small piles of corn, dyed different colours, one of which had been treated with a non-toxic bitter substance. I also assessed whether individual variation in learning ability was explained by phenotypic traits (sex, social rank and personality) and states (age and prior vigilance). I found no evidence of learning the association either within each trial or across trials, nor any variation based on individuals' phenotype. Contrary to my expectations, baboons did not exclude the consumption of unpalatable kernels within or across trials. The acceptance of unpalatable kernels suggests a high

tolerance for bitter foods in this desert population, likely exacerbated by a scarcity of preferred natural foods due to a prevailing drought. The lack of results possibly reflects baboons' prioritizing information-gathering in response to temporal habitat heterogeneity, as well as their high-tolerance for bitter foods. Finally, my findings highlight the challenges associated with conducting cognitive tests of animals in the wild.

4.2 INTRODUCTION

Learning results from past experiences which allow animals to adjust their behaviour accordingly (Shettleworth, 2010). Associative learning—a cognitive process that involves an association between stimuli and reinforcements—is key to many facets of animal behaviour (Morand-Ferron, Hamblin, et al., 2015), including fitness-related aspects such as foraging behaviour (cue preference: Ings et al., 2009; spatial memory: Schwarz & Cheng, 2010) and reproductive success (mate availability: Mahometa & Domjan, 2005). For example, in a now classic study, Dukas & Bernays (2000) used grasshoppers (*Schistocerca americana*) to demonstrate that those animals who learnt to associate stable cues signalling the presence of nutritious food, had higher growth rates than grasshoppers who were unable to learn due to being exposed to unreliable cues. The costs and benefits associated with specific cues will ultimately affect fitness by determining the speed and strength with which associations are learned (Drea & Wallen, 1999; Greenlees et al., 2010).

Associative learning may have played a such a critical role in the lives of animals that its emergence facilitated the massive diversification of life observed in the Cambrian explosion (Ginsburg & Jablonka, 2010). While differences in associative learning abilities between species are likely to reflect adaptations (Papini, 2002; Raine & Chittka, 2008), individuals within a species are also likely differ in their associative learning abilities because of differences in genotype (Galsworthy et al., 2005; Hopkins & Russell, 2014), developmental trajectory, and the environment experienced during their lifetimes (Kotrschal & Taborsky, 2010; Pravosudov et al., 2005). Recently, studies have turned their focus on individual traits, such as temperament (Sommer-Trembo & Plath, 2018), age (Morand-Ferron et al., 2015) and stress responses (Bebus et al., 2016) that likewise explain variation in associative learning.

One of the most commonly studied types of associative learning is operant conditioning, where learning is reinforced by the individual's own behaviour (Pritchett & Mulder, 2004). In his original work on operant learning, Skinner (Skinner, 1938) trained pigeons and mice to press a lever to obtain a food reward, until the animals pressed the lever continuously even in the absence of food. Research on operant conditioning, as in other areas of animal cognition, has commonly relied on devices and protocols that restrict studies to captive conditions. While captive conditions offer a controlled environment in which to test animals (Bateson, 2002; Cole et al., 2011), they may also limit the generalisability of the findings to cognition in the wild. Chapter 2 details some of the main aspects in which the methodology of captive studies may contribute to the differences in findings observed between captive and wild studies.

In this study, I investigated individual variation in the associative learning abilities of wild chacma baboons (*Papio ursinus*) by presenting individuals with an operant conditioning task that required them to associate colour with taste. Baboons, like humans, have trichromatic colour vision (i.e. they discriminate hues along the visible colour spectrum: Leonhardt et al., 2009), a trait predicted to have evolved out of the need to find ripe fruit amongst foliage (Regan et al., 2001). The task presented here reflects a biologically relevant design as baboons may use colour changes in plant foods to help assess palatability (e.g., as fruits ripen: Dominy et al., 2001) and builds on previous studies of animal learning abilities that use colour cues during foraging (e.g. yellowhead bumblebees, *Bombus flavifrons*: Dukas & Waser, 1994; common bumblebee, *Bombus terrestris*: Ings et al., 2009; hummingbirds, *Selasphorus rufus*: Samuels et al., 2014).

I first tested for evidence of learning, with my null hypothesis being that the baboons would not learn the association between the colour (red or green) and palatability (palatable or bitter) of two food choices across five presentations (trials). I tested three possible mutually-exclusive processes about how the baboons could learn the association: (1) that individuals would rapidly learn the association between the colour and taste of two food choices during the first trial, after which individuals would choose only the food associated with the palatable colour in subsequent trials; (2) that individuals would re-learn the association in each trial as independent events (failing to remember the association between trials), sampling both colours in each trial before selecting the palatable food; and (3) that individuals would gradually learn the association, improving after each trial until they either largely/completely avoided the distasteful food, or preferred to consume the palatable option before the unpalatable one. In addition, for each of the three possible learning processes, I additionally tested five hypotheses regarding the source of individual variation in the learnt association. I tested three phenotypic traits (sex, social rank, personality) and two states (age, prior vigilance) that might explain individual differences in learning ability. Refer to Chapter 3, Table 3.5, for my predictions regarding how individuals would vary in their associative learning abilities according to their phenotypic traits and their state.

4.3 MATERIALS AND METHODS

4.3.1 Study Site And Species

Fieldwork was carried out over a 6-month field season (April-September 2015) on two fully-habituated troops of chacma baboons, ranging in size from 43 (L troop) to 44 (J troop) individuals over four years of age at Tsaobis Nature Park (15° 45’E, 22° 23’S) on the edge of the Namib Desert, Namibia. All these individuals were individually identifiable. Observers accompanied both troops on foot from dawn to dusk and used Cybertracker software (www.cybertracker.org) on smart phones (Samsung Galaxy S4) to record dominance and social interactions *ad libitum*. For details on how the five individual traits were measured, as well as more details on the study species and site, please refer to Chapter 3.

4.3.2 Experimental Procedure

Individuals’ associative learning abilities were evaluated with a task in which an association between the colour (red/green) and palatability (bitter/normal) of two piles of maize corn kernels had to be learned. Across Southern Africa, chacma baboons are notorious crop raiders on maize fields (Strum, 2010), a highly desirable and nutritious food. The baboons tested here are familiar with corn kernels (albeit not coloured), having been exposed to through previous field experiments (Carter et al., 2016; King et al., 2008; Lee & Cowlishaw, 2017) and capture operations. A representative subset of 38 individuals was tested across the two troops, involving 14 adult females, 4 juvenile females, 6 adult males, and 14 juvenile males (in each case, comprising 38-66% of the identifiable individuals in that age-sex class in our study population: Chapter 3, Table 3.3). Individuals were presented with two equal amounts of dried maize kernels (approx. 20 kernels each) of different colour and palatability, and their speed of learning this association was assessed over 3-5 presentations (median: 5 presentations). Corn kernels were initially soaked overnight in either a red or green edible food colourant (Moir's Food Dye); on the following night, one of these colours was soaked again in a non-toxic concentrated bitter solution containing denatonium benzoate ('Avert', Kyron Laboratories Pty Ltd). For a similar methodology involving vervet monkeys, *Chlorocebus aethiops*, see (van de Waal, et al., 2013). Each troop was presented with a different unpalatable colour (green in J troop, red in L troop). All trials were conducted by myself and an assistant.

To avoid test subjects being displaced by dominant animals, or an audience learning socially by observing others, presentations were made to individuals when out of sight of conspecifics. Myself and an assistant moved ahead of the foraging individual and waited until it was out of sight of others, at which point the assistant, who was positioned to record the trial a few meters ahead, indicated that the trial could start. I then placed the two piles of corn on the ground ahead of the baboon while it was looking away. Each pile was approximately 10 cm in diameter and placed on the ground 10 cm apart from each other in a randomised left/right position to avoid any left/right preferences. Because trials could still be interrupted subsequently by other troop members, the same colour/palatability combination was used for all members of the same troop. All individuals received five "test" trials, each separated by intervals of three days, i.e., after the first trial (day 0), individuals were tested on days 3, 6, 9 and 12. If it was not possible to test particular individuals on the assigned day, they were tested the next possible day (re-test interval (days): mean 3.7; median 3.0). Individuals who were tested fewer than four times (n = 1) were not considered for this analysis, with the exception of those tested in the month of May (n = 9: 2 adult females, 3 adult males, 2 juvenile females, 2 juvenile males), who could only be tested in three trials due to logistical complications. All tests were conducted between sunrise (0616-0632 h during the testing period) and 1000 h (mean testing time: 0745 h) to control for motivation, as individuals are more likely to have similar levels of hunger earlier in the day. I did not test any individual who interrupted a trial and ate from either of the corn piles to avoid the confounding effects of previous experience. I took particular care that those animals that were between trials did not observe or interrupt any conspecific being tested until after their set of trials had finished. All experiments were filmed (Canon Vixia HF R300) to facilitate data extraction.

The following data were obtained from the videos for each trial: (1) the colour of the first kernel to be consumed; (2) the colour of the first ten kernels consumed; (3) the time spent eating each pile of kernels; (4) how many kernels were left (if any) from each pile; (5) the frequency of vigilance, measured as the number of times the individual scanned its surroundings; and (6) the total time dedicated to the task. Because of the context of this experiment, I expected animals would be more likely to respond to a visual cue (colour) rather than any olfactory cue associated with palatability. The latter was verified by a preliminary analysis of sniffing behaviour, also extracted from the videos that showed that sniffing behaviour, which occurred in only 21% of trials, had no relationship to the response variables evaluated here.

4.3.3 <u>Statistical Analysis</u>

All analyses were conducted in R (version 3.2.3, 2015). To test each of my proposed learning processes and their relationships to individual phenotype and state, I evaluated task performance in three ways which corresponded to the proposed learning processes respectively. First, using kernel choice (binomial, 1, Palatable; 0, Unpalatable), I investigated every choice of kernel (1-40 kernels) in trial 1 to evaluate whether individuals were capable of learning the association rapidly, within a single presentation, after which they consistently avoid the unpalatable option in subsequent trials (the latter is likewise tested in the subsequent models for trials 2-5). Second, in a similar manner, I investigated every kernel choice (1-40 kernels) for trials 2-5, using separate models in each case, to test whether learning occurs independently in each presentation. Third, I used the proportion of palatable kernels in the first 20 kernels eaten in trials 2-5 (numeric, 0-1) to test whether learning occurred gradually across trials (trial 1 was excluded as across-trial learning would only be evident in subsequent presentations, see below). I avoided testing any individual who interrupted a trial and ate from either of the corn piles.

To be able to learn the association between colour and palatability, the test subjects had to taste both types of kernel. I predicted that the baboons would have this opportunity by sampling both options at the beginning of the trial. However, this was often not the case, as the animals frequently “bulk” fed, eating one pile of corn entirely before switching to the next pile (Table 4.1). Consequently, I limited my analyses of within-trial learning to those individuals that ate from both piles within the first 20 kernels (Table 4.1, first data column). Trials interrupted by dominance interactions before individuals tasted both options available were excluded from all with-in trial analyses. However, for my analysis of across trial learning, I used all 40 kernels in trials 2-5 as I assumed that even when individuals bulk-fed they would still acquire information about both piles of kernels by the end of trial 1 (provided they fed from both, which they did), which could then be applied in subsequent presentations. Trials interrupted by dominance interactions before individuals ate at least the first 20 kernels (i.e. the amount corresponding to one pile) were excluded from these analyses.

Table 4.1 Feeding patterns for the two piles of kernels in each trial

Trial	Switch between piles within first 20 kernels	"Bulk feeding": palatable to unpalatable	"Bulk feeding": unpalatable to palatable	Interruptions
1	13	13	5	3
2	15	10	7	5
3	14	11	6	7
4	7	9	9	3
5	12	4	2	4

Shown are the number of individuals and the feeding pattern adopted in each trial. Shown are the number of individuals in each trial that: (*i*) switched between both piles presented within the first 20 kernels; (*ii*) "bulk" fed eating the correct pile of kernels in its entirety before switching to the unpalatable one; (*iii*) "bulk" fed eating the unpalatable pile of kernels in its entirety before switching to the palatable one; (*iv*) the number of trials that were interrupted before individuals could sample both pile of kernels.

I used generalised linear mixed-effects models (GLMMs) (package "lme4": Bates et al., 2015) with a logit link function to account for binomial error structure to assess the effects of phenotype and state on task performance. Individual identity was included as a random effect in all models. To facilitate convergence in all models, quantitative predictor variables were z-transformed to have a mean of zero and a standard deviation of 1. I describe each of the models in turn below.

Process 1: Rapid learning in trial 1

The analysis evaluating kernel choices within the first trial consisted of a model that addressed my questions about (a) how individuals learnt and (b) individual characteristics associated with variation in learning. As the response variable, the model (M_{T1}) included every kernel choice made (1, Palatable; 0, Unpalatable) in this trial. To test for learning, I included the kernel number as a fixed effect. I predicted that learning would be demonstrated by a positive association between kernel number and the probability of consuming a correct kernel. Additionally, I included interactions between kernel number and the sex, age, social rank and the personality of individuals. A significant interaction with any of these variables would provide evidence of phenotypic trait/state-dependent learning differences. In addition to the interactions, this model included the following three fixed effects: (1) individuals' first choice of kernel in that trial (Normal, N; Bitter: B), to control for those individuals that may have found it more difficult to detect a palatable kernel when tasting the bitter kernels first; (2) troop identity, to control for the possibility that baboons have an innate preference for a particular food colour; and (3) the probability of randomly selecting a correct kernel at each choice, to account for the change in the proportion of correct choices available as the trial progressed. This final variable was calculated as the proportion of remaining kernels that were the "correct" choice such that at the start of the trial this proportion was 0.50 (20 of 40 kernels) and was subsequently updated with each choice that was made until no choice was available (i.e. one pile had been consumed in its entirety). When individuals consumed a pile in its entirety, they were no longer able to choose between the two options; as such, the trial was considered finished after all the kernels of one pile were eaten. When trials were interrupted or individuals left kernels uneaten, a missing value was assigned to the remaining choices that were no longer possible to make. Evidence for the first hypothesis, that individuals learnt the association in the first trial and remembered the association, would involve not only a positive relationship between kernel choice and number in this model but also consistently correct choices in the subsequent trials, which are analysed in the next set of models (see below).

Process 2: Repeated rapid learning in trials 2-5

To test whether individuals re-learnt the association in each trial, I fitted four further models following the same model structure outlined in M_{T1} above for each of the subsequent trials 2-5 ($M_{T2,}$ $M_{T3,}$ M_{T4} & M_{T5}). With-in trial vigilance was no evaluated in these models as it was difficult to estimate the level of vigilance prior to each kernel choice and overall, there were not sufficient instances of vigilance for a robust analysis in each trial.

Process 3: Gradual learning across trials

Gradual learning may involve increasing the number of palatable kernels eaten across trials, until only the palatable kernels are eaten at the start of a trial. I therefore analysed the proportion of palatable kernels eaten of the first 20 kernels in trials 2-5, as this amounts to the quantity of one pile of kernels. Trial 1 was not analysed in this sample, as this was the initial learning opportunity. To test whether gradual learning was predicted by individuals' phenotypic traits/states, the fixed effects in this model included individual traits/states and their interactions with trial number (model $M_{T2\text{-}5}$). As predictor variables I included trial number and two of the same fixed effects as in the preceding models, i.e. an individual's first choice of kernels (in the first trial) and troop membership. In this model, I also evaluated past vigilance behaviour as a predictor, specifically, the frequency of vigilance instances in the previous trial, to test whether learning was negatively affected by an individual's attention being diverted from the task.

In order to assess the risk of potential collinearity between the fixed effects used in the preceding models, I evaluated Spearman correlations $|r|$ of all fixed effects used in the models. Preliminary analyses showed no co-variances where correlation coefficient was >0.70 between any of the fixed effects (Appendix S2, Table S2.1). Nevertheless, I further tested each model for multicollinearity using variance inflated factors (VIFs) (package "usdm": Naimi, 2017). As some of the fixed effects had a VIF of >2.0, I did a stepwise selection from the main model until all remaining variables had VIFs < 2.0, after which I used backwards stepwise elimination based on *p*-values until a minimum adequate model was obtained. The latter had the additional purpose of avoiding overparametrization in each model.

Interpretation of within-trial findings

Throughout the course of the experiment, the baboons adopted two unanticipated behaviours that complicated the interpretation of my within-trial learning results: bulk-feeding and consumption of the unpalatable kernels. Bulk-feeding resulted not only in reduced sampling of the available options at the start of the trials (see above), but also in reduced switching between options within trials, even if individuals had sampled both options within the first half of the trials. This affected the probability of choosing a palatable kernel as the trial progressed as one option was depleted continuously for an extended number of choices, even if it was the unpalatable choice. In addition, consumption of the unpalatable kernels meant that learning could be masked in the analyses. This is because individuals who chose the palatable kernels first and then switched to the unpalatable kernels would, counterintuitively, show a *negative* probability of choosing the correct kernels as the trial progressed, even if they had learnt the colour association and as a result were choosing the palatable option first. Because these unanticipated behaviours complicated the interpretation of the results in ways that were difficult to predict intuitively, I ran simple *post-hoc* simulations of the possible outcomes (i.e. the observed relationships between kernel choice and both kernel number and the baseline probability of choosing the palatable kernel by chance) that included the options of bulk-feeding and consumption of the unpalatable kernels to determine how I might still identify learning under these circumstances.

I ran five simulations of the different within-trial processes, two that assume within-trial learning and three that assume no learning: (1) fast learning at the start of the trial; (2) slow learning throughout the trial; (3) no learning (without bulk feeding); (4) bulk-feeding on the palatable kernels at the start of the trial; and (5) bulk-feeding on the unpalatable kernels at the start of the trial. In the first case, individuals alternately sampled two of each kernel pile to learn the association, and then ate the remaining palatable kernels before switching to the unpalatable kernels. In the second case, individuals started in the same manner as for fast learning, but progressively ate more of the palatable kernels while still intermittently sampling 1-3 unpalatable kernels until no palatable kernels remained and the unpalatable kernels were then consumed. In the third case, the choice was random. In the fourth and fifth cases, individual sampled one unpalatable or palatable kernel, respectively, first, before bulk-feeding on the other option. All scenarios were based on observations of feeding patterns in those trials in which individuals switched between piles. For each simulated scenario, I plotted the proportion of palatable kernels eaten relative to (1) the kernel number and (2) the baseline probability of choosing the palatable kernel (Fig. 4.1). I used these plots to generate expectations of what the data would look like under each scenario against which I could compare my observed results for both trials 1 (Process 1) and trials 2, 3, 4, and 5 (Process 2) (Table 4.2).

Table 4.2 Predicted learning scenarios

	Proposed scenario	**Predicted effect of kernel number on the response**	**Predicted effect of baseline probability of a correct choice on the response**
Simulations	Fast learning	Positive (weak)	Negative (weak)
	Slow learning	Positive (strong)	Negative (strong)
	No learning	None	None
	Bulk feed on correct kernels	Positive (very weak)/none	Negative (very weak)/none
	Bulk feed on incorrect kernels	Negative/none	Negative/none

Shown are the proposed learning scenarios based on simulations of the with-in trial learning process: fast-learning, slow-learning, no learning and bulk feed on correct or incorrect kernels. Columns show the expected estimates for the fixed effects of kernels and the probability of making the palatable choice.

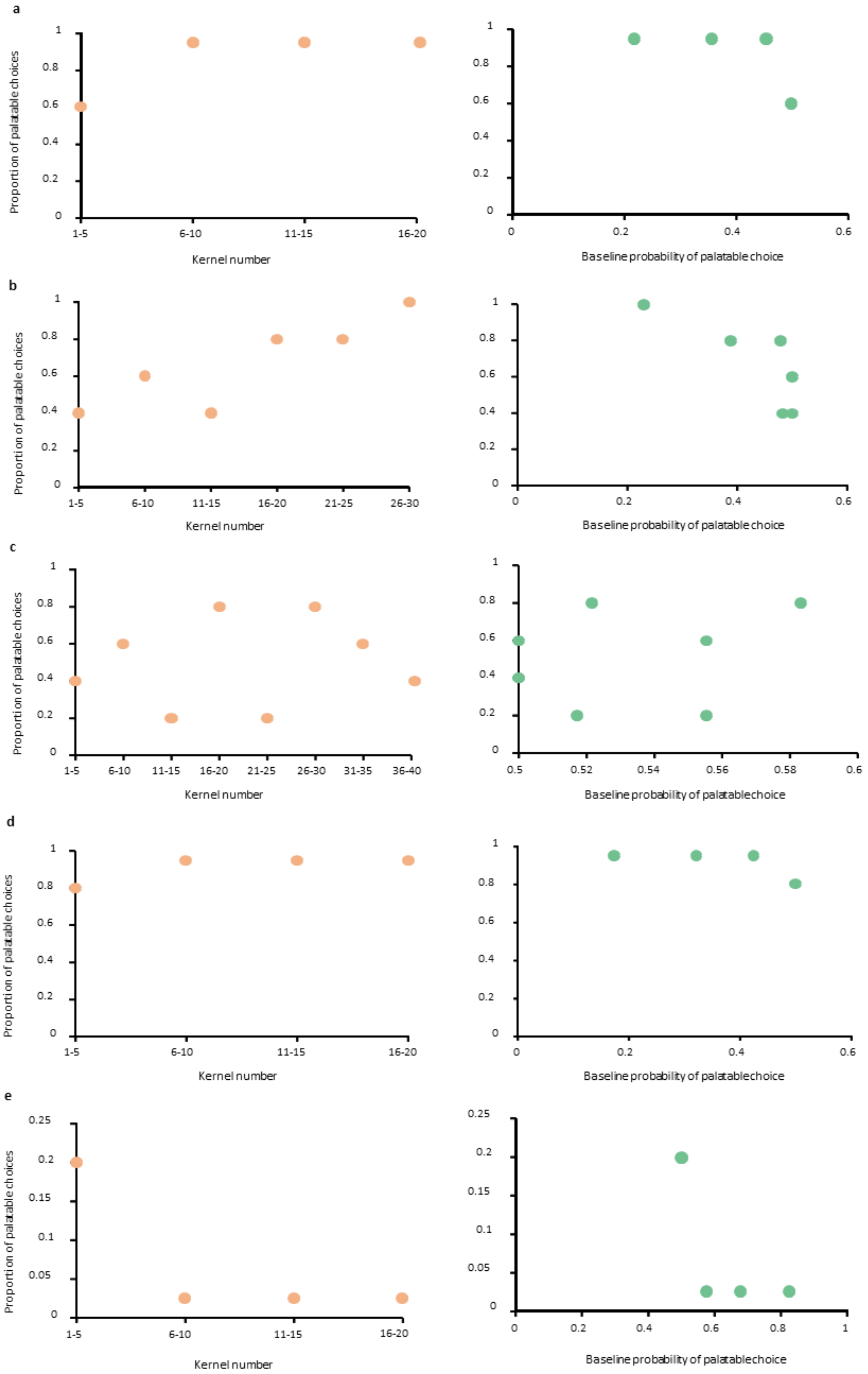
a
Proportion of palatable choices
Kernel number
1-5
6-10
11-15
16-20
Baseline probability of palatable choice
b
Proportion of palatable choices
Kernel number
1-5
6-10
11-15
16-20
21-25
26-30
Baseline probability of palatable choice
c
Proportion of palatable choices
Kernel number
1-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
Baseline probability of palatablechoice
0.5
0.52
0.54
0.56
0.58
0.6
d
Proportion of palatable choices
Kernel number
1-5
6-10
11-15
16-20
Baseline probability of palatablechoice
e
Proportion of palatable choices
0.25
0.2
0.15
0.1
0.05
0
Kernel number
1-5
6-10
11-15
16-20
Baseline probability of palatablechoice
0
0.2
0.4
0.6
0.8
1

Figure 4.1 Simulations of the learning scenarios within each trial. Each pair of plots shows the relationship between the proportion of palatable kernels eaten and the kernel number (in orange) and the proportion of correct kernels and the baseline probability of choosing a palatable kernel (in green). Shown are the expected learning scenarios for: (A) fast-learners; (B) slow-learners; (C) no learning; (D) correct bulk-feeding; (E) incorrect bulk-feeding. The proportion of palatable kernels was obtained by averaging the simulated kernel choice in groups of five. Kernel number represents the order of choice, in groups of five (i.e. group 1: kernels 1-5). The baseline probability of choosing the palatable kernels is plotted as the median probability across the five choices within each group. Note that the number of points is contingent upon how quickly the baboons completed one of the piles, after which no choice was possible and the simulation ended.

“Bulk-feeding” patterns

Two analyses were conducted to investigate the bulk-feeding patterns observed in those trials in which individuals failed to sample both piles of kernels before eating either one in its entirety. The first analysis consisted of a Chi-Sq Test of Independence, which compared the total number of trials in which individuals bulk-fed from either the palatable or unpalatable pile of kernels first to a random expectation. The second analysis consisted of a GLMM evaluating the social rank of individuals as a potential determinant for bulk-feeding behaviour. The occurrence of bulk-feeding on both piles of kernels in each trial was used as the response variable (N, No; Y, Yes); while the social rank of individuals was included as a fixed effect and individual identity as a random effect. If social rank determined bulk-feeding, I expect individuals of low-rank to be more likely to employ this behaviour, as bulk-feeding may allow such individuals to eat palatable food faster to avoid interruptions.

Both of these analyses were conducted independently of the learning scenarios proposed.

4.4 RESULTS

I tested 38 individuals over 162 trials overall (mean number of presentations = 4.3; median = 5; range 3-5). In total, 30 trials (18%) were interrupted by displacements or supplants by more dominant animals. Across all uninterrupted trials (132), the baboons consumed a median of 11 palatable kernels in the first 20 kernels (range 0-20) and eat both piles of corn in their entirety in 79 (48%) of trials. The same pattern was seen at the individual level: 12 of 22 individuals who completed five uninterrupted trials consumed all the corn in at least three of those trials. None of the individuals tested in each of the trials evaluated as subsets were interrupted before they had sampled both options. In those trials where individuals did not consume all kernels, the mean average per individual of palatable kernels remaining was 18.5 (range 18-20), in comparison to a mean average per individual of 5.5 unpalatable kernels (range 8-20). Across all trials in which individuals bulk-fed from both piles without switching between both, individuals were more likely to bulk-feed from the pile of palatable kernels first ($X^2 = 4.26$, $p = 0.03$); however, bulk-feeding behaviour was not dependent on individuals' social rank.

In my within-trial analyses (Processes 1 and 2), I found no evidence of associative learning (Tables 4.2, 4.3). My results are generally consistent with individuals using a bulk-feeding pattern after sampling with no learning (Table 4.4). The direction of this pattern is not consistent between trials however; my results show baboons favoured bulk-feeding from the unpalatable pile of kernels in three out of five trials; while in only one out of five they favoured bulk-feeding of the palatable kernels. Results in the last trial (M_{T5}) were inconsistent with any of the expected learning scenarios.

Regarding evidence of across-trial learning (Process 3), this analysis only yielded a significant relationship between the proportion of palatable kernels eaten and troop membership (Table 4.2, Fig 4.2), where individuals in L troop were more likely to eat a higher proportion of unpalatable kernels across trials than individuals in J troop. This relationship was also observed in two out of five trials (M_{T2} & M_{T3}) in the within-trial analysis. There was therefore no evidence of learning across-trials. It’s possible the former patter in the across-trial analysis was driven by these two trials.

Lastly, I found little evidence of between-individual differences in task performance. There was only one model in which an effect of phenotype was detected: an interaction between personality and kernel number was found to influence kernel choice in trial 2 (Table 4.3, $p = 0.001$) where shy individuals were found to consume the palatable kernels at the start of each trial.

Table 4.3 Learning processes and individual differences of wild chacma baboons in an associative learning task with coloured corn

Model	**Learning Process**	**Response**	**N*obs*/ N*ind***	**Deviance**	**Term**	**Estimate**	**S.E.**	***t***	***p***
M_{T1}	Process 1 Rapid Learning	Kernel Choices in Trial 1	374 / 13	476.6	Intercept	1.02	0.28	3.60	
					Kernel Number	-0.02	0.01	-2.15	**0.03**
M_{T2}	Process 2 Within-trial Learning	Kernel Choices in Trial 2	303 / 15	287.1	Intercept	2.33	0.62	3.70	
					Kernel Number	-0.03	0.02	-1.47	0.13
					Personality	-0.65	0.44	-1.46	0.14
					Troop: L[1]	-1.78	0.79	-2.25	**0.02**
					Probability of Choice	-0.69	0.39	-1.77	0.07
					K.Number*Personality	0.07	0.02	3.24	**0.001**
M_{T3}	Process 2 Within-trial Learning	Kernel Choices in Trial 3	327 / 14	332.9	Intercept	-1.67	0.65	-2.55	
					Kernel Number	0.12	0.02	5.87	**<0.001**
					Troop: L[1]	1.55	0.85	1.82	0.06
M_{T4}	Process 2 Within-trial Learning	Kernel Choices in Trial 4	154 / 7	137.6	Intercept	1.91	0.51	3.70	
					Probability of Choice	-2.32	0.67	-3.46	**<0.001**
M_{T5}	Process 2 Within-trial Learning	Kernel Choices in Trial 5	184 / 12	125.3	Intercept	-4.98	1.87	-2.66	
					Kernel Number	0.71	0.19	3.73	**0.001**
					First Choice: B[2]	3.56	1.79	1.98	**0.04**
					Probability of Choice	12.57	3.35	-3.75	**<0.001**
M_{T2-5}	Process 3 Across-trial Learning	Proportion of correct kernels in Trials 2-5	111 / 38	509.8	Intercept	2.75	0.84	3.26	
					Troop: L[1]	-2.37	1.17	-2.02	**0.04**

The table above is divided (bold lines) according to the three learning processes evaluated. Shown are: (*i*) the name of the models; (*ii*) the corresponding learning process; (*iii*) the response variable used in each model; (*iv*) the number of observations and individuals for each model; (*v*) the deviance of each model; and (*vi*) the fixed effects of the minimal models, with their effect sizes and standard errors (estimate, S.E.), test statistic (t) and *p*-values. Significant results with values of $p < 0.05$ are highlighted in **bold**. [1] Reference category: J troop. [2] Reference category: Normal kernels.

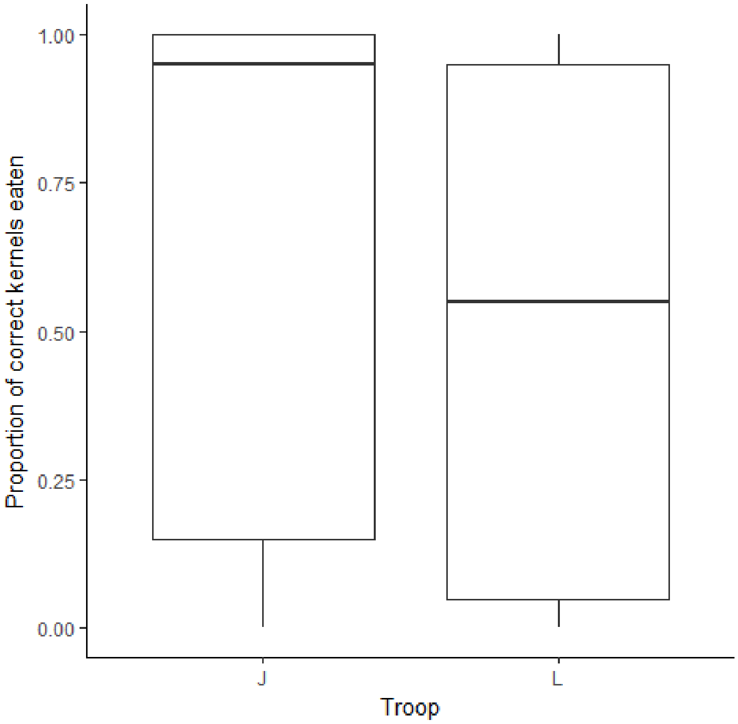

Figure 4.2 The relationship between troop membership and the proportion of palatable kernels eaten within the first 20 choices across trials 2-5. Box-and-whisker plot of the proportions of correct kernels chosen within the first 20 choices according to troop membership. The horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

Table 4.4 Observed learning scenarios within each trial

	Observed effect of kernel number on the response	**Observed effect of baseline probability of a correct choice on the response**	**Best fit scenario (from Table 4.2)**
Trial 1	Negative	None	**Bulk feed on unpalatable kernels**
Trial 2	Negative	Negative	**Bulk feed on unpalatable kernels***
Trial 3	Positive	None	**Bulk feed on palatable kernels**
Trial 4	None	Negative	**Bulk feed on unpalatable kernels**
Trial 5	Positive	Positive	**?**

The table above shows the observed scenarios of the with-in trial learning process based on the GLMM results. Refer to Table 4.2 for the predicted scenarios based on data simulations. Shown are: (*i*) the observed learning scenarios in each trial; (*ii*) the direction of the main effect of kernel number on kernel choice; (*iii*) the direction of the main effect of probability to choose the palatable kernel and kernel choice. In **bold**, the scenario and estimate observed in each trial. A question mark (?) indicates the results obtained match none of the expected learning scenarios predicted based on the estimates of the main effects of kernels number and the probability of making a palatable choice. * The interpretation of this learning scenario is complicated due to the presence of a significant interaction in the minimum model. For the purposes of comparison with the simulation output, I consider the direction of the estimate of the main effects only.

4.5 DISCUSSION

I tested the associative learning abilities of individuals belonging to two groups of wild baboons with an operant conditioning task involving an association between the colour and taste of corn kernels (red/green, palatable/unpalatable) over five trials. I expected that all individuals would show an improvement in task performance as they learned the colour-taste association either within or across trials, and that certain phenotypes/states would show faster learning than others. However, I did not find support for any of these expectations. Overall, my results suggest that individuals consistently bulk-fed in each trial, albeit there are differences between trials on whether they do so on the correct or incorrect pile of kernels. In this latter analysis, I found a single significant interaction between kernels number and personality, where shy individuals were more likely to eat the correct kernels at the start of that trial. I found that troop membership determined the likelihood of eating a higher proportion of palatable kernels across trials.

An animal's fitness may depend on its ability to make associations which persist over time (Morand-Ferron, 2017). Maintaining fitness may thus involve the ability to rapidly make associations regarding novel foods, as animals must not only determine their safety but also whether they are nutritionally rewarding (Torregrossa & Dearing, 2009; Villalba & Provenza, 2009). For instance, "one-trial" associative learning involving colour cues signalling the presence of food has been reported in primates (Guinea baboons, *Papio papio*: Lepoivre & Pallaud, 1986). Learning the colour-taste association as initially predicted (i.e. baboons would avoid the bitter kernels entirely), was not supported by my results, as not only did the majority of the baboons tested not show a consistent feeding pattern that suggested they favoured the non-bitter kernels, but they were also largely unaffected by the bitterness of the kernels. Based on this, I propose two possible explanations. The first explanation has to do with the environment in which the population under study lives. The Tsaobis environment is characterised by resources which vary in their temporal appearance and abundance (Guy Cowlishaw & Davies, 1997), but which presence is relatively reliable. In such conditions, animals benefit from learning and remembering information about familiar stimuli (i.e. their natural food sources), as re-sampling such resources may limit the time to exploit them, but extensively sample unfamiliar stimuli (Kerr & Feldman, 2003). If the latter is true for the baboons, the association was not learnt as intended, because, sampling and updating their information on each pile of kernels, is a preferred strategy. The period during which I conducted the study was additionally characterized by an intense drought (refer to Chapter 3 for further details on environmental conditions at the time field-work was conducted), which may have further promoted sampling the novel stimuli over learning.

The second possible explanation has to do with the fact that the baboons were largely unaffected by the bitterness of the kernels. It's possible the baboons rapidly learnt there was a difference in taste between both piles of kernels (i.e. one was sweet and the other was bitter). The latter may be further supported by the slight tendency of leaving bitter kernels uneaten. Generalist species such as baboons can adapt quite successfully to situations involving novel-flavoured foods (Visalberghi et al., 2003). This may be in part because they have lower gustatory sensitivity and can readily incorporate novel foods into their diet even when these are unpalatable to other species (Laska et al., 1999). Whilst bitterness is widely avoided by animals because of its association with plant toxins (i.e. plant secondary metabolites: Dominy et al., 2001), observations of chacma baboons in the Namib Desert show they readily include toxic plants (e.g. *Euphorbia avas-montana, Nicotiana glauca:* Hamilton, 1986) and immature bitter fruits (Hamilton et al., 1978) in their diet to meet their nutritional needs. Nevertheless, captive studies indicate that tolerance to bitterness varies among primate species, particularly to compounds not found in nature, such as the bitter substance used here (denatonium benzoate) (Laska et al., 2009). The variability in the abundance of resources under normal conditions, exacerbated by the extenuating circumstances of the drought, may have further influenced the test subjects' willingness to accept the bitter foods presented, as either pile of kernels represented a valuable, nutritious resource. While studies with hamadryas baboons (*Papio hamadryas*) suggest sweetness is used as a criterion to select food (Laska et al., 1999), it's likely the baboons under study have evolved a high tolerance to bitterness, perhaps as an adaptation for desert survival, which is particularly expressed during drought years when more palatable foods are unavailable (see Hamilton, 1986).

My analyses of learning across trials revealed that individuals from J troop, in which the non-bitter kernels were red, tended to eat a higher proportion of palatable corn within their first 20 choices than their L troop conspecifics. Such a result may be indicative of a species' preference for red food items. The ripening of fruit from green to red correlates with changes in their glucose level, indicating their taste quality and nutritional value (Leonhardt et al., 2009). While the normal diet of both troops includes large amounts of immature green pods, leaves and stalks, individuals who were tested could have had a natural preference for the red kernels as this colour represents a key seasonal fruit in this environment: the ripe winter berries of *Salvadora persica*. The fact that this result was only inconsistently observed within trials suggests that the preference may be a relatively weak one (unsurprisingly, given foods of both colour occur in the natural diet), and was therefore best captured by sampling individual preferences over the larger range of choices analysed in the across-trial model. Differences observed in the with-in trial analysis, may largely reflect the differences in the samples analysed. For example, results from the fifth trial did not fall within any of the learning scenarios predicted; however, one possibility may be that the majority of individuals in this sample composition were interrupted before they could complete each trial (7 out of 12 individuals evaluated were interrupted in this trial). Differences in the samples could also explain why in trial 2, there was a significant relation between kernel number and personality. According to these results, shy individuals, who in general are conservative towards novelty (Sih & Del Giudice, 2012), ate more of the palatable kernels at the start of this trial; yet, because these results were observed in a single trial, and moreover, after a prior presentation, it's difficult to determine the overall significance in the learning process.

An unanticipated aspect of baboon behaviour made this standard laboratory experiment difficult to conduct successfully in the wild, which raises further questions about the ecological validity of standard laboratory tests: the bulk feeding pattern. Because the baboons bulk fed from one pile of corn at a time, few individuals sampled both colours of corn at the start of a trial, which limited them from making an informed choice about which pile to eat. Because of this, I was forced to analyse a reduced sample, which reduced the statistical power to detect an effect. However, even when animals sampled both of the options presented, most still adopted a bulk-feeding strategy to finish each pile of kernels. Given individuals' social rank was not associated to bulk-feeding behaviour, it is unclear whether feeding in such manner is a common strategy used by baboons to consume food rapidly, but as the aggressive monopolition of high-quality resources is common in this species (Lee et al., 2016), it is possible that this bulk-feeding behaviour may be widespread in those populations that have access to maize crops given its high desirability. Moreover, it’s common for captive animals to be isolated from their group for testing (e.g. van Horik & Madden, 2016), and consequently, don’t run the risk of losing the food rewards to conspecifics. Since I offered a relatively small quantity of kernels, a highly prized food source (Refer to the “Methods and Materials” section), animals’ may have preferred this rapid technique over slower and riskier sampling, alternating between each pile of kernels. Future studies of associative learning may consider combining both stimuli, as well as providing a limited amounts of food (instead of *ad libitum* sources; e.g. van de Waal et al., 2013) to test colour-taste associations such as the one presented in this study.

My experience in developing and conducting this study reflects some of the challenges involved in devising cognitive tasks that efficiently assess cognitive abilities and suit the species under study, particularly in wild conditions. Preliminary tests in which the baboons experienced bitter and non-bitter uncoloured kernels on one occasion, saw the majority of individuals’ avoiding the bitter kernels, suggesting they were sensitive to such substance. However, it’s possible that differences in abundance of resources as well as the introduction of the colour cues resulted in the current experiment differing substantially from what was observed in the preliminary tests. My study would have benefitted from further tests not only to assess individuals’ response to cues of different intensity or traits, but to consider potential changes in behaviour relative to the environment and the resources within at different points in time. While animals commonly learn and avoid food items associated with colour cues, using information as expected may thus be dependent on the environmental conditions, as well as individuals’ diet and nutritional requirements at the time of ingestion (Villalba & Provenza, 2009). Ultimately, my study highlights the importance of using the right task to assess cognitive abilities, taking into account not only the natural behaviour of animals, but also their current environmental conditions to understand how abilities such as associative learning develop in a natural setting.

Chapter 5

An Assessment of Individual Differences and Learning Costs In Wild Chacma Baboons

5.1 ABSTRACT

The ability to learn new associations is key to many aspects of animal behaviour, including fitness-related ones such as foraging behaviour, reproduction and predator avoidance. Past research has focused on inter-species, rather than inter-individual assessments in spite of potential differences in fitness. Moreover, associative learning has mostly been restricted to studies in captivity, where the environmental and social aspects of behaviour that occur in natural circumstances that influence overall cognitive processing are often ignored. To address this, this study investigated the ability of wild baboons (*Papio ursinus*) to learn an association using stimuli—two opaque paper bags—that differed in reward. I additionally evaluated whether variation in this task was explained by a suite of phenotypic traits and/or states. My results show a relevant trade-off between exploratory behaviour and learning, as well as phenotypic differences based on sex and personality. I propose that my results reflect a foraging strategy employed by animals who live in unreliable environments with seasonal resources, where more value is given to current information rather than past experience, and individual differences determine the propensity to learn under such conditions.

5.2 INTRODUCTION

An important aspect of animal cognition is related to the ability animals have to learn novel associations. The emergence of associative learning – which consists in associating different sensory stimuli – was recently proposed to arise during the Cambrian explosion, allowing animals to make adaptive adjustments to their behaviour and exploit new resources (Ginsburg & Jablonka, 2010). Learning from past experiences and the ability to associate stimuli may allow animals to anticipate future outcomes based on the presence (or absence) of specific cues and adjust their behaviour accordingly (Ginsburg & Jablonka, 2010; Shettleworth, 2010). Past research has focused on the inter-specific comparison of a wide number of cognitive abilities, while only recently has intra-specific variation been investigated (Thornton & Lukas, 2012). This is surprising, given that individual differences can be attributed to a range of physical and social factors that persist throughout an individual's life and impact behavioural decisions and fitness consequences.

Historically, associative learning has been largely studied in captivity, as it usually requires the setup of an apparatus (Pritchett & Mulder, 2004) with which to test individuals in controlled conditions. However, captivity often places animals in highly unnatural settings (Drea, 2006), where they may be trained and tested repeatedly, often in isolation, until a success criterion is reached. This excessive exposure and subsequent habituation to man-made conditions may lead to unreliable conclusions regarding the cognitive abilities of the animals under study (van de Waal & Bshary, 2011). To understand the adaptive significance of individual variation in cognition, such behaviours must be assessed in natural conditions, particularly in the case of social species (Cronin et al., 2017).

The speed and strength with which an association is learnt depends on certain aspects of the conditions in which the stimuli are encountered. Two aspects in particular will likely determine individual performance. First, differences in the availability (i.e. always present or sometimes absent) or quality (i.e. high vs poor) of the reward when the associated stimulus is encountered will affect how quickly an association is made. Second, the presence of conspecifics will affect how much attention individuals can dedicate to a task, as some individuals have a greater risk of being displaced in a social group, which will likely affect the speed of learning. In the first case, under stable circumstances animals are expected to follow a "win-stay, lose-shift" strategy, whereby individuals learn the stimulus associated with the most rewarding option after initially experiencing both the rewarded and unrewarded stimuli (Drea, 2006). For example, a study with primates (*Papio papio:* Lepoivre & Pallaud, 1986), reported animals increased their digging for food in areas that provided food rewards over areas that did not, usually after a single encounter. Indeed, results from recent studies using discrimination tasks suggest individuals similarly follow such a strategy to successfully learn associations between colour cues, depending on the presence or absence of a reward (e.g. Ashton et al., 2018; Raine & Chittka, 2012; Shaw et al., 2015).

In the second case, while sociality often promotes cognitive development, for example, through mechanisms such as social learning (Ashton et al., 2018), living in a group comes at a cost, as animals face the risk of being recipients of aggression or kleptoparasitim (i.e. scrounging) from conspecifics over resources (Giraldeau & Dubois, 2008; Lee et al., 2016). The risk involved in participating in a task may thus be a driver of cognitive variation in those tasks involving rewards. Drea & Wallen (1999) for instance, recorded subordinate rhesus macaques (*Macaca mulatta*) successfully learning a discrimination task when tested alone, but when tested in the presence of a high-ranking individual they "played dumb", seemingly choosing not to solve the task because of the risk of losing the reward. While the latter suggests that certain traits may determine individual performance regardless of "true" cognitive ability, it is unclear whether a risky social environment promotes or constraint cognitive performance, as relatively few studies test animals in their natural social environment (c.f. Drea, 1998). The risk individuals are willing to take to participate in a task and the likelihood of successfully associating stimuli that offers a reward, are likely to be affected by individuals' current physical and social environment and physical state (Fawcett et al., 2012), as well as the phenotypic traits and states that have shaped past experiences and influence their present behaviour (Shettleworth, 2010).

In this study, I tested wild chacma baboons' (*Papio ursinus*) ability to associate cues differing in reward value, while facing risks of kleptoparasitism (i.e. interruptions from conspecifics) using a novel extractive foraging task. Following the operant conditioning task involving coloured kernels (see Chapter 4), this study was originally conceived as a generalisation task. Two paper bags, one containing corn kernels (the reward) and the other containing small rocks (the non-reward), that shared the same visual cue as the kernels (i.e. red/green colours) were presented to individuals who had previously been tested (Chapter 3, Table 3.4). However, since my prediction, that individuals would learn the association between the colour and taste of the kernels, was not supported by my results, it was implausible to assess generalisation abilities. Instead, I repeatedly presented the coloured paper bags to evaluate associative learning abilities, focusing on the costs/benefits involved in learning the association between the colour and reward of each bag. I predicted that the cost of making a wrong choice would likely vary depending on the traits of each individual, such that poor competitors—e.g. subordinates and younger individuals—who are they are at a higher risk of losing their reward due to interruptions (Drea, 1998), would more rapidly learn the association. As in the previous chapter (Chapter 4), I evaluated individual variation in learning through a common set of five hypotheses related to phenotype and state in line with my previous predictions regarding individual traits (Refer to Chapter 3, Table 3.5).

5.3 MATERIAL AND METHODS

5.3.1 Study Site And Species

Fieldwork was carried out over a 6-month field season (April-September 2015) on two fully-habituated troops of chacma baboons ranging in size from 43 (L troop) to 44 (J troop) individuals over four years of age at the Tsaobis Baboon Project in Tsaobis Nature Park (15° 45'E, 22° 23'S) on the edge of the Namib Desert, Namibia. Observers followed both groups of baboons on foot from dawn to dusk. All individuals over 4 years of age were individually identifiable. Observers moved throughout the troop, using the freely available software Cybertracker (www.cybertracker.org) on individual smart phones (Samsung Galaxy S4, Samsung, Seoul, South Korea) to record dominance and social interactions *ad libitum*. Across individuals, I classified sex, rank, and personality as phenotypic traits; and age and vigilance as states. For details on how the five individual traits were measured as well as more details on the study species and site please refer to Chapter 3.

5.3.2 Experimental Procedure

Individuals' associative learning abilities were evaluated with a task involving three presentations of two coloured paper bags in which an association between the colour (red/green) and reward value (corn/rocks) had to be learned over 3 presentations (median: 3 presentations). A representative subset of 37 individuals were tested, comprising 15 adult females, 3 juvenile females, 5 adult males, and 14 juvenile males, encompassing 40-50% of the identifiable individuals in each age-sex class in our study population (Refer to Chapter 3, Table 3.3 for further details).

Two opaque paper bags were presented on three occasions to foraging individuals. One bag contained approx. 20 corn kernels and, to avoid individuals from assessing presence of food based on the weights/volumes of the bags, the other bag contained approx. 20 small corn kernel-sized pebbles. Each bag was painted in either red or green with non-toxic children's paints, with the pebbles being associated with the incorrect colour cue and the kernels with the correct colour cue. The rewarded colour differed for each troop (green in J troop, red in L troop) to control for baboons' innate preference for a particular colour. All trials were conducted by myself and an assistant. To avoid test subjects being displaced by dominant animals before they could interact with the task, or an audience learning socially by observing others, presentations were made to individuals when initially out of sight of conspecifics. However, since the baboons were tested *in situ*, they still ran the risk of being interrupted by a conspecific. Myself and an assistant moved ahead of the foraging individual and waited until it was out of sight of others, at which point the assistant, who was positioned to record the trial a few meters ahead, indicated that the trial could start. I then dropped both paper bags on the ground ahead of the baboon while it was looking away. Because trials could still be interrupted subsequently by other troop members (see above), the same colour/reward combination was used for all members of the same troop. Individuals received a total of three “test” trials, each separated by intervals of three days, such that they were tested on days 0, 3 and 6 (where day 0 was the first presentation). If it was not possible to test particular individuals on the assigned day, they were tested the next possible day (mean; median re-test interval: 3.14; 3.00 days). No individuals were tested fewer than three times. All tests were conducted between sunrise (0620-0647 h during the testing period) and 1000 h (mean testing time: 0737 h) to control for motivation, as individuals are more likely to have similar levels of hunger earlier in the day. I did not test any individual who interrupted a trial to avoid the confounding effects of previous experience.

For each trial I recorded: (1) the colour of bag of first choice, determined as the first bag the subject touched; (2) the first bag (if any) opened, determined as the first bag from which the contents were accessed by the target individual by either tearing the bag open using both hands/mouth or turning the bags upside so that the contents fell out; (3) the exploratory time (if any) dedicated to each bag prior to and after (*i*) first contacting them and (*ii*) accessing their contents. Exploration was quantified as time spent in continuous contact with the task, including biting, sniffing or ripping apart but not statically holding it (i.e. holding it but not actively exploring it). Specific details about how exploration was measured are provided in the following section; (4) the frequency of vigilance, prior to and during contact with the bags, measured as the number of times the individual moved its gaze away from the bags to assess its surroundings. Specific details about how vigilance was evaluated are in the following section; (5) the location where the bags were placed. Specific details about how a location was defined are in the following section; and (6) the total time dedicated to the task.

5.3.3 Statistical Analysis

I used generalized linear mixed-effects models (GLMMs) fitted in R (R 3.1.1, 2014), to test individuals' ability to learn the association between the colour of bags and their respective rewards. I used three response variables to test associative learning. (1) using the first bag individuals chose (i.e. touched) in each trial (binary: 0, Incorrect; 1, Correct); (2) using the first bag individuals opened in each trial (binary: 0, Incorrect; 1, Correct); and (3) using the proportion of total exploration time they dedicated the correct bag in each trial. This last response variable was used to evaluate whether the degree of exploration was indicative of the value individuals' attributed to the bag containing the reward, reasoning that if individuals explored the correct bag longer that the alternative, they associated it with a reward. I additionally assessed whether some individuals "felt" more at risk of kleptoparasitism, by evaluating whether individuals were more likely to move the task from where it was originally placed to a potentially more secluded location, ostensibly to avoid kleptoparasitism.

To be able to choose, open and/or explore either bag, individuals had to first have contact with the task, then open at least one of the bags and decide whether to explore one or both bags. This was often not the case, however, as some animals never approach the task, and of those who did, not all opened and explored either or both bags. I subsetted my data on the basis that individuals could not learn an association between the colour and bag contents if: (a) they did not approach the bags; (b) they did not choose either one of them; and (c) they did not open and/or explore either one of them and saw their contents. Consequently, the sample size used to evaluate individuals' first choice of bag, first bag to be opened and the exploratory time given to the correct bag, included only those individuals who contacted, opened and explored either one of the bags in at least two of three trials.

1. First choice of bag

The first variable to be tested as indicative of learning was the first bag of choice individuals had in each trial. The analysis consisted of a series of models testing individuals' choice in relation to the five phenotype/state variables. First, I fitted a main model that included as fixed effects the variables of trial number and the five phenotypes/states (sex, age class, social rank, personality and vigilance). Vigilant behaviour of individuals was evaluated as the average of the vigilance rate across all trials (median = 11 instances of vigilance, range 0-38). In this model, I additionally included the fixed effect of exploratory time of both bags, predicting that highly exploratory individuals more would be more likely to choose the correct bag across trials. Exploratory behaviour was evaluated as the average of the proportion of exploratory behaviour (i.e. touched, smelled or put either bag in their mouth) of both bags across all trials (range 0 to 1 in each trial). Next to assess whether learning (i.e. predicted as a significant positive effect of trial number) was related to phenotype/state, I looked for interactions between trial number (factor: 1-3) and each of the phenotype/state variables, including exploratory behaviour ($M_{Choice*phenotype/state}$). In order to do this, but to avoid overparameterisation, I ran a separate model for each phenotype/state (including that phenotype/state variable, the trial number, and their interaction) to assess the interaction in each case except in the case of vigilance, for which no such learning relationship is predicted. Nevertheless, the frequency of vigilance instances in the previous trial was included to test whether learning was negatively affected by an individual's attention having been being diverted away from the task. The effect of vigilant behaviour on individuals' first choice of bag in each trial was calculated, for each trial respectively, as: (*i*) the frequency of vigilance from when individuals saw the task until they contacted it in the first trial; (*ii*) the frequency of the sum of vigilance instances after individuals contacted the task in the first trial and the instances prior to contacting the task in the second trial; and (*iii*) the frequency of the sum of vigilance instances after individuals contacted the task in the second trial and the instances prior to contacting the task in the third trial. In addition, I tested the effect of prior exploratory behaviour on individuals' first choice, predicting that those individuals who had higher rates of exploratory behaviour in a given trial, would be more likely to choose the correct option in the subsequent trial(s). Exploratory behaviour was measured as the proportion of time individuals spent exploring both bags. In each model, I included the additional fixed effect of troop identity, to control for the different colour assignments for pebbles/corn-filled bags between troops.

2. First bag to open

The second variable to be tested was the first bag individuals opened in each trial after contacting them. The models used (M_{Open} & $M_{Open*phenotype/state}$), followed the same structure as the models M_{Choice} and $M_{Choice*}$ described above using the first bag to be opened in each trial as a response variable. While there was no learning relationship predicted with regards to vigilant behaviour, past vigilant behaviour was included as a fixed effect to test whether learning was negatively affected by an individual's attention having been being diverted away from the task. Vigilance in this model included all instances of vigilance behaviour from when the target individual saw the task until its abandonment, excluding all vigilance instances whilst individuals were eating the kernels, to control for increases in vigilant behaviours which were independent of contact with the bags (median = 7; range 0-28). Vigilant behaviour was measured, for each corresponding trial, as: (*i*) the frequency of vigilance from when individuals saw the task until they opened either bag to access the contents in the first trial; (*ii*) the frequency of the sum of vigilance instances after individuals opened either bag in the first trial and the instances prior to opening either bag in in the second trial; and (*iii*) the frequency of the sum of vigilance instances after individuals opened either bag in the second trial and the instances prior to opening either bag in the third trial. Total exploratory behaviour was additionally used as a main effect in M_{Open} and interacting with trial number in $M_{Open*phenotype/state}$, predicting respectively that exploratory individuals would be more likely to open the correct bag first across trials or open the correct bag first in subsequent trial(s) based on prior exploration. In the first case, total exploratory behaviour was considered as the average proportion of total time during dedicated to exploring both bags (range 0 to 1 in each trial). In the second case, exploratory behaviour was measured for each corresponding trial as: (*i*) the proportion of the sum of exploratory time of both bags after accessing the inside of either bag in the first trial and the time prior to any bag being opened in the second trial; and (*ii*) the proportion of the sum of exploratory time of both bags after accessing the inside of either bag in the second trial and the time after accessing the inside of either bag in the third trial. As before, troop membership was included as a fixed effect in all models.

3. Exploratory behaviour of the correct bag

The last variable to be evaluated was the exploratory time given to the correct bag to investigate whether individuals attributed a higher value to this option by exploring it more. The analysis of the exploratory time given to the bag containing the corn reward ($M_{Explore}$ & $M_{Explore*}$), followed the same structure as the models evaluating the first bag to be opened (with the exclusion of the fixed effect of total exploratory time). The response of exploratory time of the correct bag (continuous variable, range 0 to 1 in each trial), was measured, for each corresponding trial, as: (*i*) the time each individual explored the correct bag after accessing the inside of either bag in the first trial; (*ii*) the time each individual explored the correct bag prior and after accessing the inside of the bag in the second trial; and (*iii*) the time each individual explored the correct bag prior to accessing the inside of the bag in the third trial. As before, there was no learning relationship predicted with regards to vigilant behaviour; however, past vigilant behaviour was included as a fixed effect. Vigilance in each model was evaluated in the same manner as the $M_{Open*phenotype/state}$ model. Troop was included as an additional fixed effect in all models evaluating exploration of the correct bag.

4. Risk perception

In addition to evaluating whether individuals learnt the association between colour and reward value, I evaluated the risk of kleptoparasitism associated with interacting with the task. To do this, I first fitted a GLMM was fitted to assess whether individuals of a certain phenotype or state "felt" more at risk of being the recipient of kleptoparasitism while participating in the task (M_{Risk}). As response variable, I evaluated in each trial whether individuals moved the task away from where it was initially placed towards a more secluded location (0, No; 1, Yes), reasoning that those individuals who felt more at risk would be more likely to do this to avoid kleptoparasitism. This model included the interaction between the vigilance frequency observed in the current trial and the four remaining phenotypic traits and states, as vigilance could represent an indicator of risk perception that also varies according to individual phenotype and state. Second, I used a Chi-Sq Test of Independence to test whether individuals were more likely to move the bags to a more "secluded" location, out of conspecifics' sight. To do this, the main sample was subsetted to include only those individuals that moved the bags when they were presented. The locations in which individuals were initially presented with the bags, were defined as either: (*i*) “Closed environment”, the majority of vegetation in the proximate area is clumped together and the target individual is completely blocked from conspecifics’ sight (i.e. fully secluded); (*ii*) “Semi-closed environment”, small patches of vegetation in the proximate area are clumped together in the proximate area and the target individual is somewhat secluded from conspecifics’ sight (i.e. partially secluded); and (*iii*) “Open environment”, vegetation is spread out or largely absent from the proximate area and the target individual is completely exposed to conspecifics’ sight (i.e. not secluded). This classification was likewise used to define the locations individuals moved the bags to after contacting them.

All models included baboon identity as a random effect. I used backwards elimination, dropping the least significant fixed effects until a minimum adequate model was obtained. Each of these variables was then added to the final model to check that it remained non-significant. In the case that an interaction between trial number and phenotype/state was significant, I tested all differences between levels of multilevel categorical variables (e.g. trial number) by changing the reference category sequentially and refitting the model. There were no co-variances where the Spearman correlation was $r>|0.70|$ between any of the fixed effects (Appendix S3, Table S3.1). Nevertheless, I used variance inflated factors (VIFs) to evaluate for multicollinearity and did a stepwise selection for each model until all remaining variables had a VIF < 2.0.

5.4 RESULTS

I evaluated the associative learning abilities of individuals using three measures: (1) the first choice of bags in each trial; (2) the first bag they opened; and (3) the proportion of exploratory time of the correct bag in each trial. I completed 111 trials across 37 individuals (mean number of presentations = 3; median = 3), after which, the sample was subsetted to include only those individuals that had contacted and interacted with the bags in at least two out of three trials (n = 87 trials across 29 individuals).

5.4.1 First Choice Of Bags

Overall, only one of our study subjects (1 adult female) failed to approach any of the bags in two out of three trials; while 8 study subjects failed to open either one of the bags in two out of three trials. Individuals chose the correct bag on 45 out of 87 (51.7%). On 5 separate occasions (4.6% of trials), individuals failed to make a choice on a given trial because they did not approach either one of the bags; and on 2 occasions (1.8% of trials), there was no clear choice between the bags, as they picked up both of them at the same time. No trial was interrupted before individuals could make a first choice of bag. Analysis of these patterns yielded a significant interaction between the boldness level of individuals and trial number, with bolder individuals being more likely to first choose the incorrect bag, however this effect was only observed between trial 1 & 2 ($M_{Choice*Bold}$, Fig. 5.1). See Table 5.1 for these results.

5.4.2 First Bag To Be Opened

In the data subset used to evaluate the first bag to be opened and the proportion of exploratory time dedicated to exploring the correct bag, 29 out of the 37 of the baboons tested approached, opened and explored either one of the bags in at least two out of three trials. Only in 8% of trials individuals did not open either one of the bags. In the case of those individuals that did, the correct bag was opened on 40 out of 87 trials (46%). Individuals had an average median exploratory time of both bags 23 s (range 0-147). The correct bag was explored a median average of 12.5 s (range 0-97); while the incorrect bag was explored a median average of 11 s (range 0-57). Trials were interrupted on 30 out of 87 occasions (34% of the total sample) and only 9% trials were interrupted before individuals could access the contents and/or explore either one of the bags. Following their exclusion, analyses of these patterns revealed a negative relationship between trial number and the bag that was opened first (M_{Open}, Fig 5.2), as well as between and the total exploratory time and bag that was opened first (M_{open}, Fig 5.3). Individuals were more likely to choose the incorrect bag in trial 3 compared to their choice in trial 2. A similar trend was likewise observed between trials 1 and 3; however, this did not achieve statistical significance. Moreover, those individuals who on average were more exploratory of both bags, were less likely to open the correct bag (Table 5.1).

5.4.3 Exploration Of The Correct Bag

In the evaluation of the proportion of exploratory time dedicated to the correct bag as evidence of a successful association between bag colour and contents, I found a significant interaction between trial number and both sex ($M_{Explore*Sex}$, Fig 5.4) and boldness ($M_{Explore*Bold}$, Fig 5.5). In the first case, females had a higher exploratory time of the correct bag compared to their male conspecifics, although this difference was only significant in trial 3. In the second case, shyer animals (i.e. with a lower boldness score), had a higher exploratory time of the correct bag, albeit only in trial 3. Refer to Table 5.1 for these results.

Table 5.1 GLMM analyses of the individual differences of wild chacma baboons in an extractive foraging task with coloured bags.

Model	**Response**	**N*obs*/ N*ind***	**Deviance**	**Term**	**Levels**	**Estimate**	**S.E.**	***z***	***p***
$M_{Choice*Bold}$	First choice of bag	84/29	110.6	Trial	Trial 2 (ref: Trial 1)	-0.04	0.59	-0.07	0.93
					Trial 3 (ref: 1)	-0.08	0.59	-0.15	0.87
					Trial 1 (ref: 2)	0.04	0.59	-0.07	0.94
					Trial 3 (ref: 2)	-0.04	0.58	-0.07	0.94
				Boldness	Boldness (ref: 1)	0.72	0.51	1.39	0.16
					Boldness (ref: 2)	-0.68	0.47	-1.45	0.14
				Trial* Boldness	Trial 2: Boldness (ref: 1)	-1.41	0.69	-2.02	**0.04**
					Trial 3: Boldness (ref: 1)	-0.86	0.64	-1.33	0.18
					Trial 1: Boldness (ref: 2)	1.41	0.69	2.02	**0.04**
					Trial 3: Boldness (ref: 2)	0.54	0.60	0.91	0.36
M_{Open}	First bag to open	72/29	90.5	Trial	Trial 2 (ref: Trial 1)	0.18	0.61	0.29	0.32
					Trial 3 (ref: 1)	-1.04	0.62	-1.66	0.09
					Trial 1 (ref: 2)	-0.18	0.61	-0.29	0.76
					Trial 3 (ref: 2)	-1.22	0.61	-1.99	**0.04**
				Total Exploration		-0.59	0.26	-2.25	**0.02**
$M_{Explore*Sex}$	Exploration of the correct bag	73/29	377	Trial	Trial 2 (ref: Trial 1)	0.57	0.38	1.47	0.13
					Trial 3 (ref: 1)	0.51	0.40	1.24	0.21
					Trial 1 (ref: 2)	-0.57	0.38	-1.47	0.14
					Trial 3 (ref: 2)	-0.06	0.26	-1.24	0.81
				Sex: Male[1]	Sex (ref: 1)	0.97	0.46	2.10	**0.03**
					Sex (ref: 2)	0.16	0.29	0.55	0.57
				Trial* Sex	Trial 2: Sex (ref: 1)	-0.81	0.44	-1.84	0.06
					Trial 3: Sex (ref: 1)	-1.09	0.47	-2.32	**0.02**
					Trial 1: Sex (ref: 2)	0.81	0.44	1.84	0.06
					Trial 3: Sex (ref: 2)	-0.28	0.32	-0.85	0.39
$M_{Explore*Bold}$	Exploration	73/29	379	Trial	Trial 2 (ref: Trial 1)	**0.18**	0.23	0.77	0.44
					Trial 3 (ref: 1)	**0.01**	0.25	0.03	0.96
					Trial 1 (ref: 2)	**-0.18**	0.23	-0.77	0.43
					Trial 3 (ref: 2)	**-0.17**	0.21	0.80	0.42
				Boldness	Boldness (ref: 1)	**0.005**	0.004	1.29	0.19

	Boldness (ref:2)	**-0.001**	0.003	-0.55	0.58
Trial* Boldness	Trial 2: Boldness (ref: 1)	**-0.007**	0.004	-1.85	0.06
	Trial 3: Boldness (ref: 1)	**-0.009**	0.004	-2.02	**0.04**
	Trial 1: Boldness (ref: 2)	**0.007**	0.004	1.85	0.06
	Trial 3: Boldness (ref: 2)	**-0.001**	0.003	-0.50	0.61

Shown are: (*i*) the names of the models; (*ii*) the number of observations and individuals for each model; (*iii*) the deviance of each model (*iv)* the fixed effects of the minimal models, with their effect sizes and standard errors (estimate, S.E.), test statistic (t) and *p*-values. Significant results with values of $p < 0.05$ are highlighted in **bold.** [1] Reference category: female.

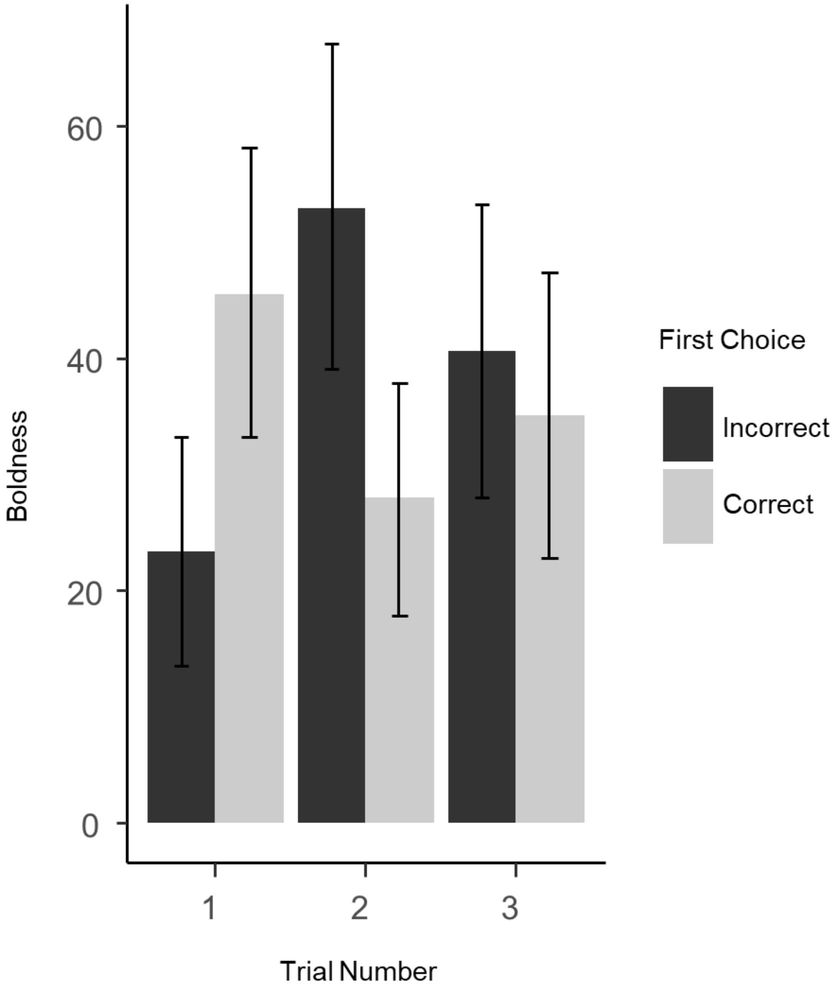

Figure 5.1 The interaction between the first choice of the correct bag and the trial number and boldness of individuals (N = 29). Shown is a barplot of the interaction between boldness and the first bag chosen in each trial (1-3). The first choice was calculated as a binary variable, where 0 indicates an incorrect choice and 1 the correct choice, and is indicated by dark grey and light grey bars, respectively, while boldness was used as an index for personality and assessed as the time spent exploring a novel food item (range 0-120, with bolder individuals indicated by higher scores). Mean and standard error bars are shown.

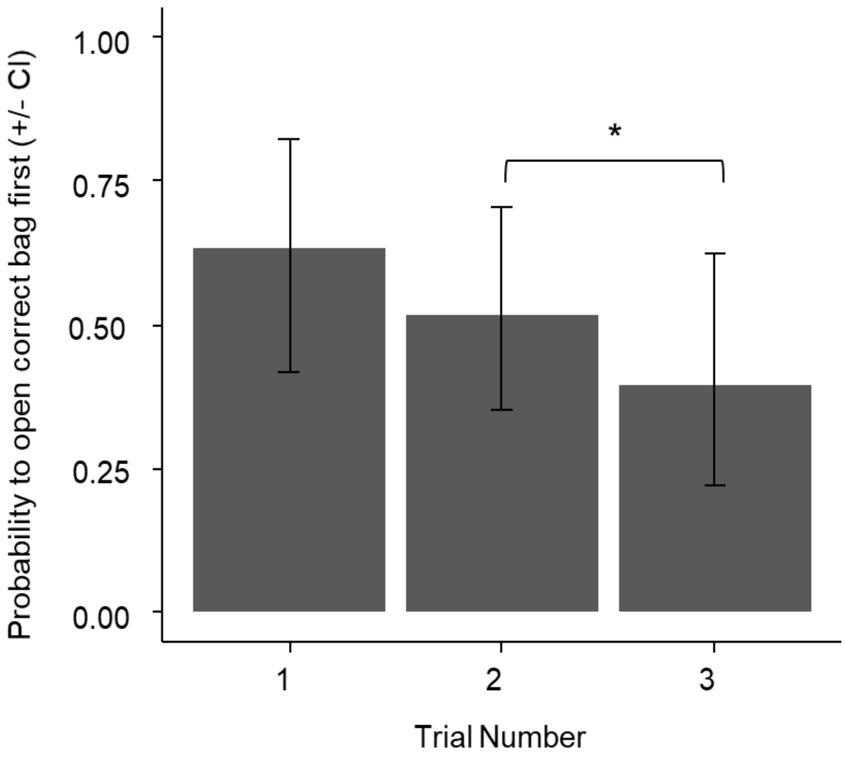

Figure 5.2 The probability of opening the correct bag first across trials (N = 29). Shown is a bar plot of the probability of opening the correct bag first across trials (1-3). The first bag opened is calculated as a binary variable, where 0 indicates an incorrect choice and 1, a correct one. Error bars represent 95% confidence intervals. The asterisk indicates a significant (p = <0.05) difference between the trials.

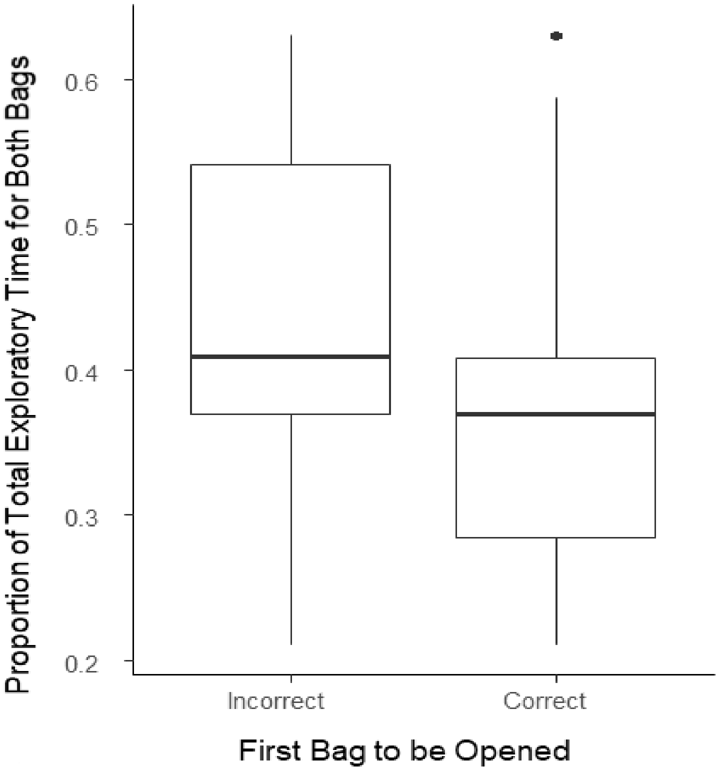

Figure 5.3 The proportion of total exploratory time dedicated to both bags and the first bag to be opened (Correct; Incorrect) (N = 29). Shown are box and whisker plots of the first bag opened and the total proportion of exploratory time given to both bags. First bag opened is calculated as a binary variable, where 0 indicates an incorrect choice and 1 the correct choice, while total exploratory time was measured as the total time individuals spent exploring both bags in each trial (1-3). The horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

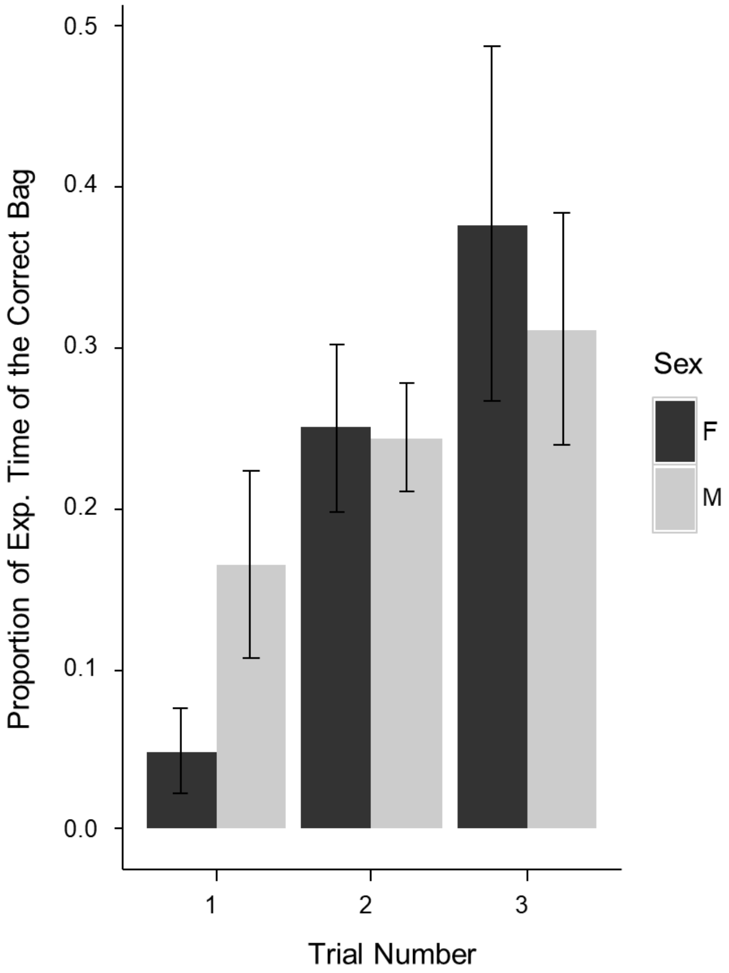

Figure 5.4 Shown is a barplot of the interaction between the proportion of total exploratory time dedicated to the correct bag in each trial and trial number and sex (N = 29). The proportion of exploratory time dedicated to the correct bag was measured as the exploratory time given to the correct bag after accessing its contents in each trial (1-3). Columns coloured in dark grey and light grey indicate individuals' sex (F, Females; M, Males). Mean and standard error bars are shown.

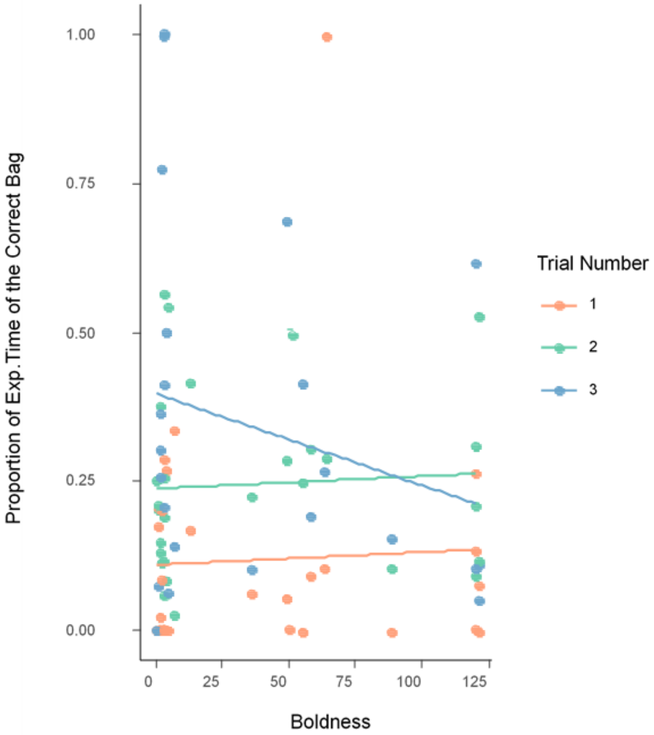

Figure 5.5 Shown is a scatterplot of the interaction between the proportion of total exploratory time dedicated to the correct bag in each trial and trial number and boldness (N = 29). The proportion of exploratory time dedicated to the correct bag was measured after the contents of the bags had been accessed in each trial (1-3). Boldness was used as an index for personality and assessed as the time spent exploring a novel food item. A trend line was fitted according to the trial number for each trial (see legend).

5.4.4 Risk Perception

Finally, in 46 out of 111 (41%) trials, individuals took either one or both bags and moved away from the area from where they were first presented. I assessed whether certain phenotypes and/or states were more likely to move away as an indicator of perceived risk (Table 5.2). Analyses of these patterns revealed no significant interactions between the vigilance rate individuals had during testing and their phenotype traits and state (*p* = >0.05). However, I did find that moving the bags to a secluded location in each trial was dependent on age and social rank, where juveniles and low-ranking individuals were more likely to move the bags away.

On 46 trials individuals moved the task from the area where it was first presented. On 9 occasions, the task was initially presented in a “Close environment” location; on 25 occasions in a “Semi-closed environment”; and on 12 in an “Open environment”. The environment were the bags were first presented, did not predict whether animals moved the bags to a “secluded” environment after they were presented ($X^2 = 0.64$, $p = 0.72$). However, the general trend indicates that animals moved the bags to another, similar environment, rather than changing to a completely different environment.

Table 5.2 GLMM results assessing the phenotypic and state differences in risk perception in the extractive foraging task.

Model	N*obs*/ N*ind*	Deviance	Term	Estimate	S.E.	z	p
			Intercept	-2.83	1.18	-2.39	
			Vigilance	-3.96	3.75	-1.05	0.08
M_{Risk}	106 / 37	94.2	Boldness	-1.70	0.96	-1.77	0.07
			Age: Juvenile[1]	4.81	1.18	2.63	**0.008**
			Social Rank	-2.52	0.89	-2.81	**0.004**
			Vigilance*Bold	7.47	4.21	1.77	0.07

Shown is: (*i*) name of the model; (*ii*) the number of observations and individuals for the model; (*iii*) the fixed effects of the minimal model, with their effect sizes and standard errors (estimate, S.E.), test statistic (t) and *p*-values; and (*iv*) the deviance of the model. Significant results with values of $p < 0.05$ are highlighted in **bold.** [1]Reference category: Adult

5.5. DISCUSSION

In this chapter, I assessed baboons' ability to form an association between cues that differed in reward value while facing social risk. Evidence for associative learning was evaluated by investigating whether: (1) individuals' first choice of bag to handle; (2) individuals' first choice of bag to open; and (3) the exploratory time dedicated to the correct bag in each trial improved over three trials. My results provide partial evidence of learning based on the exploratory time dedicated to the correct bag; bolder individuals and males explored the correct bag proportionally less than the shyer individuals and females respectively in the third trial. Additionally, because of the way the task was presented and the difference in reward content in each bag, some individuals may have been more restricted than others in their opportunity to interact with the task due to possible interruptions from conspecifics. Thus, I additionally investigated whether there were differences in individuals' perceived risk of kleptoparasitism when solving the tasks, evidenced by individuals moving the bags to a more secluded location before exploring them, as. In this case I found that more vulnerable individuals—low-ranking and younger individuals—were more likely to move away with the bags. Moreover, the characteristics of a location did not predict whether individuals would choose a more "secluded" location in which to solve the task after moving the task.

Regarding individuals' first choice of bag, I found that bolder animals were more likely to choose the correct bag in the first trial and the incorrect bag in the second trial compared to shyer individuals. Animals that are bold are usually more successful in cognitive tasks (Carter et al., 2014; Ducatez et al., 2015) as they readily approach novel stimuli and sample their environment more rapidly compared to shyer individuals (Guillette et al., 2009; Trompf & Brown, 2014). However, it is unclear why bold animals were more likely to choose the correct bag in the first trial. Although shyer individuals were more likely to switch to the correct choice in the second trial, given that there was no difference in the boldness of individuals who made a correct choice in the third trial, it is likely that the results of the first two trials arose by chance. Below I consider some limiting factors of the experimental design that could have contributed to such an outcome.

In evaluating the first bag that was opened, I found that individuals were less likely to open the correct bag first in trial 3 compared to their second trial. In addition, those baboons that were more exploratory of both bags were less likely to open the correct bag, regardless of the trial. Learning requires individuals to acquire information about their environment and subsequently use that information to make decisions. It is commonly expected that lower exploration of a stimulus leads to less accurate decision-making (Eliassen et al., 2007) and previous studies assessing exploration in cognitive tasks have indeed found that less exploratory animals are usually outperformed by their more exploratory conspecifics (e.g. problem solving: Benson-Amram & Holekamp, 2012; innovation: Miller et al., 2016). However, environments are not always uniform or predictable in their abundance of resources (i.e. homogeneous environments: Kerr & Feldman, 2003) and animals may make decisions that prioritise regularly updating information in unpredictable environments. Such a strategy would avoid individuals' use of outdated information, but this would be at the cost of the time involved in constantly sampling the environment. My results suggest that this could be the case for this test, as the baboons were experiencing a drought at the time of testing and they continued to explore both bags during all three tests. Future studies could empirically test this hypothesis by re-testing the baboons in a more stable period.

In this task I observed that sex and personality predicted the exploratory time dedicated to the correct bag in trial 3 when compared to the first trial. Studies assessing cognitive abilities have often found task-specific differences between sexes (Boose et al., 2013; Vallortigara, 1996). For example, Vallortigara (1996) found that females were better in colour learning, while males outperformed them in a position learning task. Such differences may be determined by the environment each sex experiences (Dingemanse et al., 2004), as well as personality (e.g. *Corvus corax*: Range et al., 2006; *Parus major*: Titulaer et al., 2012). Females in this study had a relatively low exploratory behaviour of the correct bag in the first trial, which then rapidly increased in the subsequent trials. Such a response perhaps reflects a normal neophobic response, not unlike what has been observed in other studies with primates (*Pan troglodytes*: Hopper et al., 2014). However, differences between the sexes in this case might also have to do with the immediate fitness benefits of investing in collecting information to learn a colour-reward association, as most females either had to care for a dependent infant during pregnancy and lactation or sustain an estrous swelling. All these activities are costly and may be particularly so in an unstable environment. In the case of personality, shy animals spent proportionally longer exploring the correct bag than their bold conspecifics. However, this relationship was only seen in the last trial, which suggests that the neophobic response ultimately extinguishes and careful exploration over time may indeed result in more accurate choices.

The variation observed in moving the bags to a different location in this task suggests that some individuals are, or have been, more susceptible to aggression and felt more at risk while participating in the task. This is because less competitive individuals i.e. juveniles and low-ranking animals, were more likely to move the bags than more competitive individuals. These observations raise the question of whether social competitiveness promotes or constrains individuals from learning associations. Given that neither one of my learning results depended on the age or social rank of the individual baboons, it seems likely that in a risky social environment, the strategies that the less competitive individuals adopted mitigated the possible costs of receiving aggression, and did not limit these individuals' learning compared to more competitive individuals (see: Drea, 1998). Another possibility may be that poor competitors, who commonly forage on the periphery of the group, are vulnerable to other types of pressures, such as predation (Cheney et al., 2004) and consequently, move the task to a location that is less exposed. Information on individuals' spatial position within the group at the time of testing was not possible to obtain; however, the given that in the majority of occasions individuals did not move the bags to a different environment from the one they were presented in, a more likely explanation may be that individuals simply look to avoid any aggression from conspecifics in the immediate surroundings from where the bags were placed. Ultimately, how "secluded" a location was considered to be, depended on the test subject's point of view and its knowledge of conspecifics' position.

As in my previous chapter, my results highlight some of the common challenges involved in testing wild animals with cognitive tasks, such as having a low number of observations per individual. Presenting a task repeatedly remains a challenge in any cognitive study in the wild (Morand-Ferron et al., 2015). It is possible that if the trials progressed beyond the three provided here, individuals would eventually spend less time in exploration and a more obvious learned response would be apparent. In addition, studies that have used similar discrimination tasks to evaluate associative learning often only allow animals to make a single choice before removing the task and the alternative option (e.g. Ashton et al., 2018; Shaw et al., 2015). Such a study design excludes behaviours that may be adaptive but may be common, such as exploration of the alternative choice, and presents a situation that may not be ecologically relevant. I consider this study a first step to understanding how wild animals make trade-offs between information gathering for learning novel associations and investing in safer, more immediately-rewarding behaviours to optimize their own fitness.

Chapter 6

Learning Through Second-Order Conditioning In Wild Chacma Baboons

6.1 ABSTRACT

Second-order conditioning, a type of classical conditioning, consists of making indirect associations between stimuli via another association. While second-order conditioning has been shown to be widespread through multiple experiments with animals, so far none has tested animals in the wild; therefore, its occurrence has yet to be examined in a natural setting. In this chapter, we tested wild chacma baboons with a second order conditioning task which included three testing phases: (1) the pairing of a food stimulus (corn kernels) with a clicker; (2) the pairing of a neutral stimulus with the same clicker; and (3) the presentation of the neutral stimulus on its own. Over the course of one day, each individual was presented with the stimuli three times in each of the corresponding phases, resulting in a total of nine trials. We also tested two control groups, in which the stimulus in either the first or second phase was presented independently of the clicker. At the end of the experiment, the baboons failed to demonstrate second-order conditioning: our experimental group exhibited the same response to the neutral stimulus as our control groups in the third phase. We discuss some of the methodological challenges that may have caused

these results and compare them to the approaches that have been commonly used in captive experiments.

6.2 INTRODUCTION

Pavlovian or Classical conditioning is a form of associative learning which consists in modifying a behaviour by strengthening the association between two stimuli (Gallistel et al., 2004; Rescorla, 1980). This is achieved by pairing a “neutral” stimulus, the conditioned stimulus (CS), to a motivational reinforcer or unconditioned stimulus (US), usually associated with a biologically important reward. Eventually, the individual will respond to the CS alone resulting in a conditioned response (Gallistel et al., 2004; Shettleworth, 2010). This is commonly referred to as first-order conditioning. A common example of classical conditioning is Pavlov’s original work on the salivation response of a dog when presented with food. By ringing a bell prior to the presentation, the dog’s response to the bell was eventually the same as its response to the food (Pavlov, 1927). Classical conditioning has since been used to investigate a number of topics, from cognition (e.g. Giurfa & Sandoz, 2012; Shors, 2001) to fitness-related traits, such as reproductive success (e.g. Hollis et al., 1989; Mahometa & Domjan, 2005) and foraging performance (e.g. Hollis et al., 2004).

Animals are able to make and maintain a variety of biologically relevant associations throughout their lifetime (Hussaini et al., 2007). Some are straightforward, such as when animals have a direct experience with the stimuli, while others are made indirectly, via other learnt associations. As research on conditioned responses expanded, it became clear that it was possible to learn various relationships across significant events, even when the US was not present (Rescorla, 1980). Second-order conditioning, a form of classical conditioning, represents such a case in which a new stimulus can replace the US in a significant event (Rescorla, 1980). It consists of first pairing an US with a conditioned stimulus (CS1), as in Pavlovian conditioning, but the CS1 is then paired with a neutral stimulus (CS2) with the expectation that this second stimulus will be equally associated with the US (Holland & Rescorla, 1975; Rescorla, 1980). Classical conditioning can be theoretically limited, as individuals are usually exposed to situations in which they encounter the US beforehand (Crawford & Domjan, 1995) and even in cases where individuals have limited experienced, the US has to be innately excitatory (i.e. produce a response even before pairing it with a CS) for the behaviour to be reinforced. In contrast, second-order conditioning can occur in situations that do not involve an excitatory US; instead, a novel CS can serve as a reinforcer due to previous learning events involving a US (Rescorla, 1980). Previous research in both humans and other animals, has commonly approached second-order conditioning from a psychological point of view, exploring the extinction of the CS (*Rattus spp.*: Holland, 1980); the overlapping of stimuli (*Gerbillinae*: Maisiak, 1977); and the effects of second-order conditioning on causal learning tasks (humans: Jara et al., 2006) to name a few. Other studies with animals have instead focused on evaluating the efficiency of aversive stimuli (e.g. pidgeon, *Columbia livia*: Rashotte et al., 1981) and appetitive stimuli (e.g. goldfish, *Carassius auratus*: Amiro & Bitterman, 1980), finding both are equally likely to result in second-order conditioning.

The ability to make second-order associations seems to be widespread in nature, as shown in studies on numerous animal taxa including and invertebrates (bumblebee, *Bombus terriestris*: Dawson et al., 2013; bee, *Apis mellifera*: Hussaini et al., 2007; fruit fly, *Drosophila melanogaster*: Tabone & de Belle, 2011), fish (Amiro & Bitterman, 1980; zebra danio fish, *Brachydanio rerio*: Hall & Suboski Milton, 1995), birds (Japanese quail, *Coturnix japanica*: Crawford & Domjan, 1995; *Columbia livia*: Marshall et al., 1979; Rashotte et al., 1981) and primates (mangabey, *Lophocebus* spp*:* Findley et al., 1966) . The range of species in which second-order conditioning has been shown suggests there is an ecological significance in making second-order associations. For instance, Hall & Suboski (1995) found that exposure to stimuli through second-order conditioning elicited antipredator alarm reactions in zebrafish, suggesting that the ability to extend stimulus characteristics can be adaptive. More recently, second-order conditioning has been used to study ecologically relevant behaviours in social species. Work with invertebrates, for example, has focused on the use of social stimuli (i.e. social learning) as a means to learn associations (see Dawson et al., 2013), as social species might be adapted to prioritize cues from conspecifics. Despite the growing literature on associative learning, second-order conditioning experiments have yet to be applied to a wild population. Studies in the wild that mirror those in captivity are likely to be difficult to achieve due to the extensive training and often high number of trials required. However, conducting experiments in the natural environment of a species may increase our understanding of its ecological validity, particularly in social species (see Cronin et al., 2017 for an example in primates).

Given the wide range of species in which second-order conditioning has been observed, it is possible Pavlovian conditioning, including second-order conditioning, constitutes a common process through which animals learn new associations. The present study was conducted to determine whether wild chacma baboons (*Papio ursinus*) can learn to associate stimuli through second-order conditioning. Second-order responses may be ecologically relevant in this species, as it potentially allows individuals to use past knowledge of conspecifics' interactions with food resources (e.g. Dawson et al., 2013) and/or predators (e.g. Mineka & Cook, 1988) to exploit or avoid novelty respectively. I approached this study by first presenting individuals randomly assigned to either a control or an experimental group, with a pairing of stimuli consisting of corn kernels and a clicker; second, by presenting a pairing of a clicker and a neutral stimulus, in this case, a blue square; and third, by presenting the neutral stimulus on its own. While social cues (e.g. a conspecific demonstrator) would have been relevant to this study, using a particular conspecific repeatedly as a stimulus was methodologically unfeasible. If baboons can learn through second-order conditioning, i.e., if individuals can correctly associate the CS1 (a clicker) with both the US (corn kernels) and CS2 (cardboard square), then I expect individuals in our experimental group to: (1) have a shorter latency time to approach the CS2 when presented on its own; and/or (2) to be more exploratory (i.e. touching, biting, sniffing) of the CS2 when presented on its own.

6.3 MATERIALS AND METHODS

6.3.1 Study Site And Species

This study was carried out over a 5-month-long field season (May-September 2016) on two fully-habituated troops of chacma baboons ranging in size from 53 (J troop) to 60 (L troop) individuals at the Tsaobis Baboon Project at Tsaobis Nature Park (15° 45’E, 22° 23’S) on the edge of the Namib Desert, Namibia. Chacma baboons were chosen as a model species for this work because, as a robust terrestrial primate species, they are tractable for field experiments. For more information on this species and the two study troops please refer to Chapter 3.

6.3.2 Experimental Protocol

A total of 27 individuals were tested, involving 13 adult females, 1 juvenile female, 3 adult males, and 10 juvenile males. This was a representative sample of our study troops, comprising 33-50% of the identifiable individuals (all animals over four years of age) in each age-sex class in our population (Chapter 3, Table 3.3). Each individual received the stimuli on nine separate occasions separated into three phases (hereafter referred to as Phases I, II and III) over the course of a single day. Each phase involved three presentations (hereafter referred to as trials) with an average inter-trial interval (ITI) of 57 min (range 20-227 min), such that a full assessment lasted approx. nine hours in total. Individuals were tested out of sight of conspecifics. All task presentations and observations were conducted by myself.

Study subjects were allocated randomly into three groups, each with nine individuals, according to whether or not stimuli were presented together (paired) or separately (unpaired) in the first two phases: Paired-Paired (P-P, Group 1); Paired-

Unpaired (P-U, Group 2); and Unpaired-Paired (U-P, Group 2) (Table 6.1). The P-P Group was the experimental group as they were given the opportunity to learn the associations between both the US and CS1, and the CS1 and CS2, before being tested on whether they made the association between the US and CS2. The P-U and U-P Groups served as control Groups as they were able to learn only one association, between the US and CS1 or the CS1 and CS2, before being tested on whether they made the association between the US and CS2. I describe each phase in further detail below.

Table 6.1 Experimental design of the second-order condition task

Group	Group Composition	Phase I	Phase II	Phase III
P – P	Sex (F/M): 5/4 Age (J/A): 4/5 Rank (H/M/L): 3/3/3	**Clicker (CS1) + Corn (US)** Subjects learn to associate the clicker with a food reward	**Clicker (CS1) + Square (CS2)** Subjects learn to associate the clicker with a neutral stimulus	**Test CS2** Subjects can associate the food reward with the neutral stimulus
U – P	Sex (F/M): 4/5 Age (J/A): 3/6 Rank (H/M/L): 5/3/2	**Clicker (CS1) ~ Corn (US)** Control	**Clicker (CS1) + Square (CS2)** Subjects learn to associate the clicker with a neutral stimulus	**Test CS2** Subjects cannot associate the food reward with the neutral stimulus
P – U	Sex (F/M): 5/4 Age (J/A): 3/6 Rank (H/M/L): 3/3/3	**Clicker (CS1) + Corn (US)** Subjects learn to associate the clicker with a food reward	**Clicker (CS1) ~ Square (CS2)** Control	**Test CS2** Subjects cannot associate the food reward with the neutral stimulus

Shown are the groups, the composition of the sample of individuals tested in each group, the order of the presentation of stimuli, and the rationale for those presentations, in each phase of the experiment. The composition of each group is shown according to sex (F, females; M, males), age (J, juveniles; A, adults) and social rank (H, high rank; M, medium rank; L, low-rank). Social rank categories were assigned according to tertiles. A plus symbol (+) indicates that the stimuli were presented together, a tilde (~) indicates a 10 min separation in the presentation of the stimuli (the stimulus presented first was randomised for each trial). See text for details of the conditioned stimuli 1 and 2 (CS1 & CS2).

Phase I

Phase I represented a simple first-order conditioning task. Trials in this phase began approx. at 0700 h for all individuals. For the P-P and P-U Groups, I paired a small pile of corn kernels (approx. 20) (US) with a clicker trainer (CS1) (Beaphar, Suffolk, UK). Corn kernels were used as a US for two reasons: first, because individuals in this population had experience with such food items prior to this study (e.g. Lee & Cowlishaw, 2017; Marshall et al., 2012); and second, because as a highly desirable resource (Strum, 2010), baboons have a strong excitatory response towards them. The clicker was pressed once the kernels had been deployed, and immediately after the subject had seen the kernels, and pressed repeatedly every second until all the corn was consumed. If a trial was interrupted by aggression from any other animal (i.e. supplant, displacement or attack of the animal eating the kernels), the clicking immediately stopped (see Table 6.2 for interruption frequencies), at which point the trial was considered completed. In this phase, the U-P Group experienced unpaired presentations, where the clicker was presented by repeatedly clicking it for 10 s either 10 min before or after the corn was presented. The order of the corn and clicker was alternated between trials. If it was not possible to present the corn or the clicker (depending on which was presented first) for instance if the baboon was then in the presence of conspecifics at exactly 10 min after, the appropriate stimulus was presented at the next possible chance (this occurred in 19 of 27 cases, median 10 min, range 6-14 in this Phase). Throughout this phase I recorded in every trial: (1) the latency to approach the corn kernels, measured as the time it took individuals to contact the kernels after first seeing them; (2) the time spent eating the corn kernels; (3) the time dedicated to exploring the ground around the corn kernels, considered as the use of both hands or visual scans to search the immediate area of substrate on which the kernels was placed; (4) the reaction of the baboon to the clicker, measured as either, for P-P and P-U Groups, the number of times the baboon lifted its head from the corn kernels when the clicking started and turned its head towards the source of noise (i.e. myself) or, for the U-P Group, the number of times the baboons turned their head towards the source of noise; (5) the number of vigilance scans, when the baboon lifted its head to scan its surroundings without looking in the direction of the clicker; (6) any aggressive interruption of the trial; and (7) the total time of the trial (s).

<u>Phase II</u>

Phase II began approx. one hour after Phase I ended (median 53 min, range 40-224). Here, I paired the clicker (CS1) with a neutral stimulus, a 17 x 17 cm cardboard square painted blue with non-toxic children’s paint (CS2) for both P-P and U-P Groups. A blue cardboard square was chosen as a CS2 because by definition, the neutral stimulus should not be known to test subjects, nor should it provoke any excitatory or preconditioned response (Rescorla, 1980). This pair of stimuli was presented three times over three consecutive trials. In this phase, the P-U Group experienced unpaired presentations, where the clicker was presented 10 min before or after the CS2 in the same manner as Phase I. If it was not possible to complete the trial exactly 10 min after, for instance if the baboon was then in the presence of conspecifics, the second presentation (of either the clicker or the CS2, depending on which was presented first) was conducted at the next possible chance (21 cases, median 11 mins, range 6-27). I allowed a maximum of 5 min (300 s) for the individual to approach and interact with the CS2, starting after it was determined as “seen” by the individual. Given that the stimulus’ colour contrasted with the natural surroundings and it was generally placed on an exposed location (i.e. not amongst vegetation), I was able to determine whether and when the CS2 was “seen” based on the sustained or repeated movement of individuals’ head and/or gaze towards ITS immediate direction (i.e. approx. 1m radius around the CS2). My proximity and clear view of individuals’ facial features further allowed me to accurately estimate the direction of their gaze. If the baboon did not interact with it within this time, I considered the trial finished. Likewise, if a trial was interrupted by a conspecific supplanting, displacing or attacking the focal animal, all measurements stopped, and the trial was considered finished. In this phase I recorded for every trial: (1) the latency to approach the CS2, quantified as the time it took individuals to contact the CS2 after first seeing it. (2) the time spent exploring the CS2 (s), measured as the time individuals spent in continuous contact with the task, including biting, sniffing and statically holding it (i.e. holding it but not actively exploring it); (3) the time dedicated to exploring the ground around the CS2, considered as time spent using both hands or visual scans to search the immediate area of substrate on which the CS2 was placed; (4) the reaction of the baboon to the clicker, measured as either, for the P-P and U-P Groups, the number of times the baboon lifted its head from the stimulus when the clicking started and turned its head towards the noise (i.e. myself), or for the P-U Group, the number of times the baboons turned their head towards the noise; (5) the number of vigilance scans; (6) any aggressive interruption of the trial; and (7) the total time of the trial (s).

Phase III

Phase III began approx. one hour after Phase II ended (median 60 min, range 20-122). Here, baboons in all groups were presented with the blue cardboard square (CS2) on its own. The CS2 was presented three times over three consecutive trials. In this phase, as in Phase II, once the CS2 was seen, I allowed a maximum of 5 min for the test subject to approach and/or interact with it and considered the trial ended after this time had elapsed. Likewise, if a trial was interrupted by a conspecific supplanting, displacing or attacking the focal animal, all measurements stopped and the trial was considered finished. In this phase I recorded: (1) the latency to approach the CS2 (s); (2) whether the baboon interacted with the CS2 (i.e. approached and touched); (3) the time spent exploring the CS2 (if any); (4) the time dedicated to exploring the ground around the CS2; (5) the number of vigilance scans; (6) any aggressive interruptions of the trial; and (7) the total time of the trial (s).

6.3.3 Statistical Analyses

The analyses were completed using the R environment (version 3.2.3, 2015) in two steps. First, I assessed the evidence for second-order conditioning, by testing whether, during Phase III, the latency to approach the CS2 was shorter, and the time spent exploring the CS2 was longer, in the P-P Group than in either the P-U or U-P Groups. Refer to the "Experimental Protocol" to see how these variables were quantified. In the case of latency to approach, I fitted two Cox proportional hazards regressions, one to analyse trial 1 of Phase III (Trial III.1) alone (<u>M</u>odel.<u>P</u>hase3$_{\text{T1-Laten}}$), the second to analyse trials 1-3 (III.1, III.2, III3) together in Phase III (M.P3$_{\text{Laten}}$). In a similar manner, for exploratory time, I used a general linear model (GLM) to analyse trial 1 (M.P3$_{\text{T1-Explor}}$) and a generalised linear mixed model (GLMM) to analyse trials 1-3 in Phase III (M.P3$_{\text{Explor}}$). In all models, the predictors were treatment Group (P-P, U-P, P-U), trial number and its interaction with treatment Group (where multiple trials were included; M.P3$_{\text{Laten}}$ and M.P3$_{\text{Explor}}$). Individual ID was included as a frailty term in the cox regression or as a random effect in the GLMM to control for repeated measures on individuals across trials. As mentioned previously, I predicted P-P subjects should show shorter latencies and longer exploratory times than the control subjects in trial 1 of Phase III. My expectations across trials 1-3 in Phase III was that the P-P subjects would either sustain their learnt association, evidenced by a significant effect of treatment Group but no significant interaction between treatment Group and trial number, or the association would gradually be extinguished as they failed to find corn kernels with the blue square, evidenced by a significant fixed effect of treatment group and an interaction between treatment Group and trial number. No individual explored of the area surrounding the CS2 in this Phase.

The Cox proportional hazard models were fitted using the “survival” package (Therneau & Lumley, 2014). Survival models, such as Cox proportional hazards regressions, are a valuable tool in time-to-event data analyses (Jahn-Eimermacher et al., 2011), as they permit ceiling values to be included as censored data points in those cases where individuals did not approach the task (Dean et al., 2011). In cases where individuals did not interact with the stimulus but moved away from it before reaching the 5 min limit, the latency was marked as the total trial time from when the individual saw the stimulus until it moved away and marked as a censored data point. Altogether, 17 individuals in 28 trials failed to approach the CS2 in Phase III. In the case of exploration of the CS2, to evaluate exploration of the stimulus in the first trial of Phase III I fitted two models. First, a GLM ("lme4" package: Bates et al., 2015) with a quasi-Poisson distribution to account for over-dispersion. Second, a GLMM with a Poisson distribution to evaluate exploratory behaviour of the CS2 across trials and test Groups, included in this models as an interaction. To account for over-dispersion in this model, Observation-Level Random Effects were included as an additional random effect. If the interaction between Group membership and trial number was found to be non-significant, it was dropped from the model and each variable was evaluated independently. The eliminated interaction was then added back to the final model to check it remained non-significant. Lastly, I used a Chi-Square Test of Independence to test whether the probability of sniffing and biting the CS2 was determined by Group membership.

To further investigate the second-order conditioned process, I evaluated individuals' response to the paired stimuli presented in each of the first two Phases of the experiment. In the second stage of the analysis, I went on to explore the latency to approach the stimulus and exploratory behaviour in Phases I ($MP1_{Explor}$) and II ($MP2_{Late}$ & $MP2_{Explor}$). In Phase I, I excluded any analyses regarding the latency to approach the US (i.e. the pile of corn kernels) as all individuals contacted the corn kernels extremely rapidly (median latency of 2 s, range 0-45); instead, I assessed only the exploratory time given to the area around the US, i.e. the conditioned response. Additional models were fitted to assess: (1) whether the pairing of the CS1 and US resulted in a successful first order association, in which case I would see a higher rate of exploration of the area around the US for the P-P and P-U Groups as these Groups received both stimuli paired; and (2) whether the lack US in Phase II resulted in an early extinction of the CR prior to Phase III, in which case, I would expect to see individuals of the U-P Group to have a lower exploratory rate of the CS2, as well as a lower exploratory of the CS2 as trials progress for all individuals as this groups did not experience paired stimuli in the previous Phase. I used the same approach to analyse latency and exploratory times in Phases I and II as in the analyses of Phase III. No individual explored of the area surrounding the CS2 in any of these Phases. Table 6.2 shows a summary of Phases I, II and III models design.

Table 6.2 Summary of model design for each Phase (I, II and III)

	Model	Justification	Response	Fixed Effects
Phase I	$MP1_{Explor}$	Establish first-order conditioning	Exploration of the area around the US (i.e. the CR)	Trial Number* Group
Phase II	$MP2_{Late}$	Evaluate early extinction of the CR	Latency to the CS2	Trial Number* Group
	$MP2_{Explor}$	Evaluate early extinction of the CR	Exploration of the CS2	
Phase III	$MP3_{T1\text{-}Laten}$	Establish second-order conditioning	Latency to the CS2	Trial Number* Group
	$MP3_{T1\text{-}Explor}$	Establish second-order conditioning	Exploration of the CS2	
	$MP3_{Laten}$	Establish second-order conditioning	Latency to the CS2	Trial Number* Group
	$MP3_{Explor}$	Establish second-order conditioning	Exploration of the CS2	

Shown are: (*i*) the name of each corresponding Phase; (*ii*) the name of each model; (*iii*) justification for each model; (*iv*) the fixed effects used. Variables marked with an asterisk (*) indicate interactions between that fixed effect (i.e. Trial Number) and the effects listed underneath.

For the third stage of this analysis, I looked into the determinants of first-order conditioning in Phase I, as this process is key to developing a successful second-order response. To do this, I fitted an additional six GLM models with a quasi-Poisson distribution to evaluate two possible variables—vigilance and CS1 duration—that could have affected the formation of a CR, i.e. exploration of the area around the US, in each of the three Phase I trials (I.1, I.2 & I.3), Groups that received the paired stimuli in Phase I (P-P and P-U Groups). For the set of models evaluated vigilance and CS duration respectively I tested: (1) whether vigilant behaviour during each trial reduced the attention given to the cues in the first-order association; and (2) whether the duration of the CS1 whilst animals were eating the kernels affected the formation of the first-order association. In the first case, if animals were more vigilant, I would expect to see a weaker response to the CS (i.e. less exploration) as vigilance often deviates attention from other activities (Fragaszy & Visalberghi, 1990). The models testing the effect of vigilance on the CR ($MT1.1_{Explor*Vig,}$ $MT1.2_{Explor*Vig}$ & $MT1.3_{Explor*Vig}$) included an interaction between vigilant behaviour in that trial and treatment Group (i.e. P-P and P-U) as a fixed effect. As mentioned previously, vigilance was evaluated as the number of instances in which test animals lifted their heads to look around while being tested (median duration of 15 s, range 1-130); however, since I was unable to distinguish individuals' response to the clicking noise and their general vigilant behaviour, I excluded from this measurement any instances in which the test animals looked directly at myself, the source of the clicking. The total time of the trial (s) was included as an additional fixed effect to control for trial duration. In the second case, if animals were exposed to the CS1 (i.e. the clicker) for a shorter period, I would expect to see a weaker CR, as a shorter time of the clicking noise may have gone unnoticed or failed to reinforce the association. Models testing the duration of the CS1 on the CR, ($MT1.1_{Explor*CS1}$ $MT1.2_{Explor*CS1}$ & $MT1.3_{Explor*CS1}$), included an interaction between the duration of the CS1 in that trial and treatment Group as a fixed effect. The duration of the CS1 (s) was measured from the time the clicking noise started to when it ended (median duration of 15 s, range 1-130). Lastly, in Phase II, I used a Chi-Square Test of Independence to test whether the probability of sniffing and biting the CS2 was determined by Group membership. If the latter was true, then I would expect to see higher rates of sniffing and biting in those individuals of the P-P and P-U Groups compared to the U-P Group. Table 6.3 provides a summary of the models described above.

Table 6.3 Summary of model design for each additional prediction in Phase I

	Model	Justification	Response	Fixed effects
Trial I.1	$MT1.1_{Explor*Vig}$	Distraction from the stimuli due to vigilance	Exploration of the area around the US	Group* Vigilance
	$MT1.1_{Explor*CS1}$	Duration of the CS1		Group* Length of CS1
Trial I.2	$MT1.2_{Explor*Vig}$	Distraction from the stimuli due to vigilance	Exploration of the area around the US	Group* Vigilance
	$MT1.2_{Explor*CS1}$	Duration of the CS1		Group* Length of CS1
Trial I.3	$MT1.3_{Explor*Vig}$	Distraction from the stimuli due to vigilance	Exploration of the area around the US	Group* Vigilance
	$MT1.2_{Explor*CS1}$	Duration of the CS1		Group* Length of CS1

Shown are: (*i*) the name of each corresponding Phase; (*ii*) the name of each model; (*iii*) justification for each model; (*iv*) the fixed effects used. Variables marked with an asterisk (*) indicate interactions between that fixed effect (i.e. Trial Number) and the effects listed underneath.

6.4 RESULTS

I completed 243 trials conducted across 27 baboons, with each baboon receiving 9 trials over three test Phases (see Table 6.4 for descriptive statistics for each group). I did not find evidence of second-order conditioning based on the evaluation of Group differences in trial III.1 and the interaction between trial number (1-3) and Group in both our assessments of the latency to contact and subsequent exploration of the CS2 in Phase III (Tables 6.5 & 6.6). There was no tendency for the P-P subjects to show a shorter latency ($M.P3_{T1Laten}$, P-U: $p = 0.68$, U-P: $p = 0.88$; $M.P3_{Laten}$: P-U: $p = 0.62$, U-P: $p = 0.91$) or greater exploratory time ($M.P3_{T1Explor}$, P-U: $p = 0.29$, U-P: $p = 0.21$; $M.P3_{Explor}$: P-U: $p = 0.83$, U-P: $p = 0.19$) in Phase III in comparison to the

U-P or P-U subjects. Fig 6.1 shows the latency to approach and exploratory time of the CS2 across trials in each group in Phase III.

Since we did not find evidence of second-order conditioning, we went on to assess whether the baboons learnt the first order association presented in Phase I. I predicted a longer exploration of the area around the US by those individuals who experienced a pairing of stimuli in Phase I. I also tested whether the response to the CS2 became extinct during Phase II. Evidence for this would be that the baboons showed longer latency times and less exploration of the CS2 depending on Group membership and Trial number. In the first case, I found a significant relationship between Trial number and Group membership in our analysis of Phase I. In contrast to my prediction that only the groups that received the paired stimuli in Phase I would show greater exploration of the area around the US, individuals from the P-U and U-P Groups had higher exploration than the P-P group in both Trials I.2 and I.3 (Table 6.6, Fig 6.2). I found no evidence that either vigilant behaviour or the duration of the CS1 affected the CR in any trial for Groups P-P and P-U (Table 6.7).

Table 6.4 Descriptive statistics of each of the Groups (P-P, U-P, and P-U) in Phase I, II and III.

	Parameter	**P-P**	**U-P**	**P-U**
Phase I	Latency to approach US – median (range), s	2 (0-45)	2 (0-16)	6 (0-15)
	Exploratory time of area around US – median (range), s	5.5 (0-67)	7 (0-27)	8 (0-61)
	Time eating US – median (range), s	13 (0-33)	13 (2-29)	12 (6-46)
	Number of head turns towards CS1 – median (range)	1 (0-2)	1 (0-3)	0.9 (0-4)
	Aggressive interruptions – n/n_{total}, %	9/27, 33%	11/27, 40.7%	4/27, 15%

	Parameter	**P-P**	**U-P**	**P-U**
Phase II	Latency to approach CS2 – median (range), s	8 (0-187)	8 (1-300)	8.5 (2-300)
	Interaction with the CS2 – Yes/No, n trials	23/4	19/6	21/6
	Biting of the CS2 – Yes/No, n trials	19/8	9/16	13/14
	Sniffing of the CS2 – Yes/No, n trials	21/1	18/7	18/9
	Exploration time of CS2 median (range), s	13 (0-184)	4 (0-69)	5 (2-159)
	Number of head turns towards CS1 – median (range)	1 (0-5)	1 (0-3)	1 (0-3)
	Aggressive interruptions – n/n_{total}, %	1/27, 3.7%	11/27, 40.7%	3/27, 11.1%
Phase III	Latency to approach CS2 – median (range), s	7 (1-300)	6 (1-300)	11 (1-300)
	Interaction with the CS2 – Yes/No, n trials	23/4	16/11	16/11
	Biting of the CS2 – Yes/No, n trials	10/17	6/21	6/20
	Sniffing of the CS2 – Yes/No, n trials	17/10	13/14	13/13
	Exploration time of CS2 median (range), s	3 (0-109)	2 (0-235)	2 (0-98)
	Aggressive interruptions – n/n_{total}, %	1/27, 3.7%	2/27, 7.4%	2/27, 7.4%

Each group consists of N = 27 observations across N = 9 individuals (females: 15/male: 12; adults: 17/juvenile: 10). Depending on the Phase, shown here are: (1) the median ($\tilde{x}$) and range of the latency to approach the US or the CS2; (2) the exploratory time of the area around the US, the time spent eating the corn kernels (i.e. US); (3) whether individuals interacted with the CS2 and the exploratory time given to it, including the number of times individuals sniffed and bit the CS2; (4) the median of times individuals turned their heads due to the clicker noise (CS1); and (4) the total number of aggressive interruptions observed, including the percentage it represents of the total trial number.

Table 6.5 Minimum adequate models obtained from the Cox proportional hazards analyses of factors affecting latency of baboons to approach and contact the CS2 in Phases II & III

	Coefficient	**S.E. of Coefficient**	**Chi-sq**	**Df**	***p***	**CI (+/-)**
M.P2$_{\text{Late}}$						
Group: PU[1]	-0.46	0.46	0.99	1	0.32	0.25/1.56
Group: UP[1]	-0.51	0.45	1.30	1	0.25	0.24/1.45
Frailty (Individual)			21.35	11	0.34	
N*obs*: 78, N*events*: 62, Variance of random effect = 0.37, I-Likelihood = -220.5, Likelihood ratio test = 35.9 on 12.3 df, *p* = 0.00004						
M.P3$_{\text{T1-Late}}$						
Group: PU[1]	0.25	0.63	0.40		0.68	0.37/4.49
Group: UP[1]	-0.08	0.56	-0.14		0.88	0.30/2.76
Nobs: 78, *Nevents*: 53, Variance of random effect = 0.31, I-Likelihood = -1.96, Likelihood ratio test = 26.01 on 10.56 df, *p* = 0.005						
M.P3$_{\text{Late}}$						
Group: PU[1]	-0.21	0.44	0.24	1	0.62	0.33/1.91
Group: UP[1]	-0.05	0.45	0.01	1	0.91	0.39/2.29
Frailty (Individual)			14.36	9	9.41	
Nobs: 18, *Nevents*: 18, Rsquare = 0.015, Concordance = 0.54 Likelihood ratio test = 27 on 2 df, *p* = 0.87						

Cox proportional hazards model results of the latency to approach the CS2 in Phases II &III. Shown are: (*i*) name of the models; (*ii*) the covariates assessed; (*iii*) the regression coefficients; (*iv*) the standard errors (S.E.) of the regression coefficient (*v*) Chi-square values; (*vi*) degrees of freedom (Df); (*vii*) *p*-values; and (*viii*) the upper and lower 95% confidence intervals (CI (+/-)) for the hazard ratio. Significant results with values of $p < 0.05$ are highlighted in **bold.** [1] Reference category: P-P Group.

Table 6.6 Minimum adequate models investigating the individual differences of baboons of three Groups in a SOC task, where the response variables were: (1) the proportion of time exploring the area around the US in Phase **I**; (2) the proportion of time exploring the CS2 in Phase **II**; and (3) the proportion of time exploring the CS2 in Phase **III** in the first trial and in trials 1-3.

Model	**N_{Obs} / N_{Ind}**	**Deviance**	**Term**	**Estimate**	**S. E.**	**z**	**p**
M.P1$_{\mathbf{Explor}}$	72 / 27	467.4	Intercept	2.71	0.43	6.19	
			Trial: **I**.2[1]	-1.54	0.40	-3.76	**<0.001**
			Trial: **I**.3[1]	-1.53	0.37	-4.11	**<0.001**
			Group: PU[2]	-0.83	0.65	-1.27	0.20
			Group: UP[2]	-0.90	0.66	-1.35	0.17
			Aggression Received: Y[3]	-1.14	0.28	-3.95	**<0.001**
			Trial: **I**.2*Group: PU	1.59	0.57	2.77	**0.005**
			Trial: **I**.3*Group: PU	1.93	0.56	3.42	**<0.001**
			Trial: **I**.2*Group: UP	2.01	0.62	3.20	**0.001**
			Trial: **I**.3*Group: UP	1.60	0.58	2.75	**0.005**
M.P2$_{\mathbf{Explor}}$	63 / 26	471.2	Intercept	3.44	0.32	10.54	
			Trial: **II**.1[4]	-0.48	0.20	-2.35	**0.01**
			Trial: **II**.3[4]	-1.30	0.23	-5.61	**<0.001**
			Group: PU[2]	-0.75	0.44	-1.68	0.09
			Group: UP[2]	-0.93	0.46	-2.02	**0.04**
M.P3$_{\mathbf{T1\text{-}Explor}}$	27 / 27	175.6	Intercept	2.75	0.33	8.30	
			Group: PU[2]	-0.80	0.73	-1.09	0.29
			Group: UP[2]	-0.76	0.58	-1.30	0.21
M.P3$_{\mathbf{Explor}}$	24 / 53	368.9	Intercept	1.71	0.30	5.64	
			Trial: **III**.2[5]	-0.07	0.35	-0.20	0.83
			Trial: **III**:3[5]	0.47	0.36	1.31	0.19

Shown are: (*i*) name of the models (see text for details); (*ii)* the number of observations and individuals in each model; (*iii*) the deviance of each model; (*vi*) the explanatory variables used in each model (i.e. fixed effects)and (*v*) the significance of each fixed effect, determined by *p*-values. In **bold**, are p-values = <0.05. [1] Reference category: Trial I.1. [2] Reference category: P-P Group. [3] Reference category: No. [4] Reference category: Trial II.1. [5] Reference category: Trial III.1

Table 6.7 Minimum adequate models investigating the individual differences of baboons CR in Phase I in the P-P and P-U Groups in a SOC task, where the response variables was: (1) the proportion of time exploring the area around the US.

Model	N_{Obs} / N_{Ind}	Deviance	Term	Estimate	S. E.	*t*	*p*
MT1.1$_{\textbf{Explor*Vig}}$	16/ 16	83.52	Intercept	1.25	0.61	2.05	
			Vigilance	0.06	0.10	0.67	0.51
			Group: PU^1	-1.56	1.80	-0.86	0.40
			Total time of trial	0.02	0.008	2.76	**0.01**
			Vigilance*Group: PU	0.05	1.17	0.31	0.75
MT1.2$_{\textbf{Explor*Vig}}$	17/ 17	104.6	Intercept	2.00	0.75	2.64	
			Vigilance	-0.004	0.12	-0.03	0.96
			Group: PU^1	-0.50	1.23	-0.41	0.68
			Total time of trial	-0.01	0.01	-0.90	0.38
			Vigilance*Group: PU	0.22	0.20	1.07	0.30
MT1.3$_{\textbf{Explor*Vig}}$	16/ 16	156.6	Intercept	1.19	0.86	1.67	
			Vigilance	0.009	0.11	0.07	0.94
			Group: PU^1	0.35	1.13	-0.32	0.75
			Total time of trial	0.009	0.005	1.62	0.13
			Vigilance*Group: PU	0.10	0.14	0.73	0.48
MT1.1$_{\textbf{Explor*CS1}}$	16/ 16	283.6	Intercept	1.21	1.56	0.77	
			CS1	0.10	0.08	1.29	0.22
			Group: PU^1	0.99	1.77	0.56	0.58
			CS1*Group: PU	-0.08	0.08	-1.07	0.30

			Intercept	1.30	1.34	0.97	
MT1.2$_{\mathbf{Explor*CS1}}$	17/ 17	118.6	CS1	0.02	0.08	0.25	0.80
			Group: PU[1]	1.07	1.39	0.77	0.45
			CS1*Group: PU	-0.02	0.08	-0.23	0.82
			Intercept	1.19	1.21	0.98	
MT1.3$_{\mathbf{Eplor*CS1}}$	16/ 16	156.6	CS1	0.03	0.05	0.59	0.56
			Group: PU[1]	0.93	1.33	0.70	0.49
			CS1*Group: PU	-0.006	0.06	-1.11	0.91

Shown are: (*i*) name of the models (see text for details); (*ii)* the number of observations and individuals in each model;; (*iii*)the deviance of each model; (vi) the explanatory variables used in each model (i.e. fixed effects)and (*v*) the significance of each fixed effect, determined by *p*-values. In **bold**, are p-values = <0.05. [1]Reference category: P-P Group.

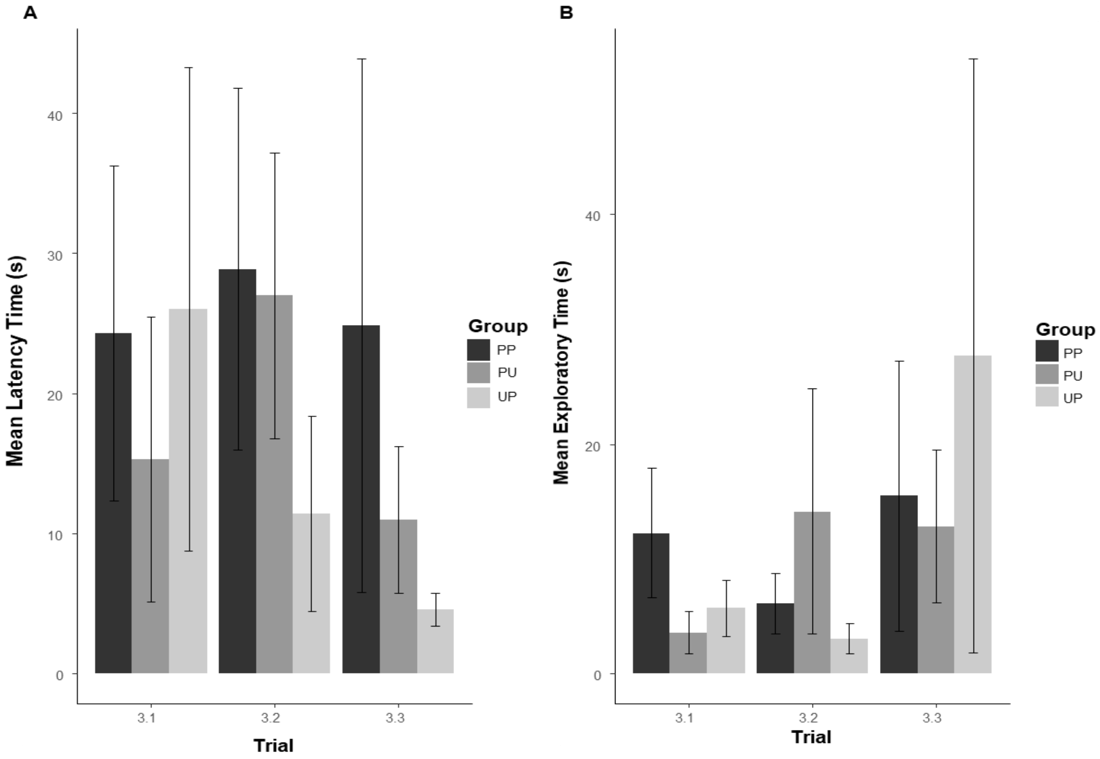

Figure 6.1 The interaction between (**A**) the latency to approach the CS2; and (**B**) the mean exploratory time of the CS2 and Trial Number (**III**.1-**III**.3) and the Group individuals were assigned to in Phase **III** (N = 27). Latency was measured as the time it took individuals to approach the CS2 from when they first saw it until contact. Exploration was measured as the time individuals spent exploring the CS2 (i.e. the blue square), including handling, sniffing or biting; while group membership consisted of whether the CS1 and the US were paired or unpaired in Phases **I** & **II** (see legend). Means and standard error bars are shown.

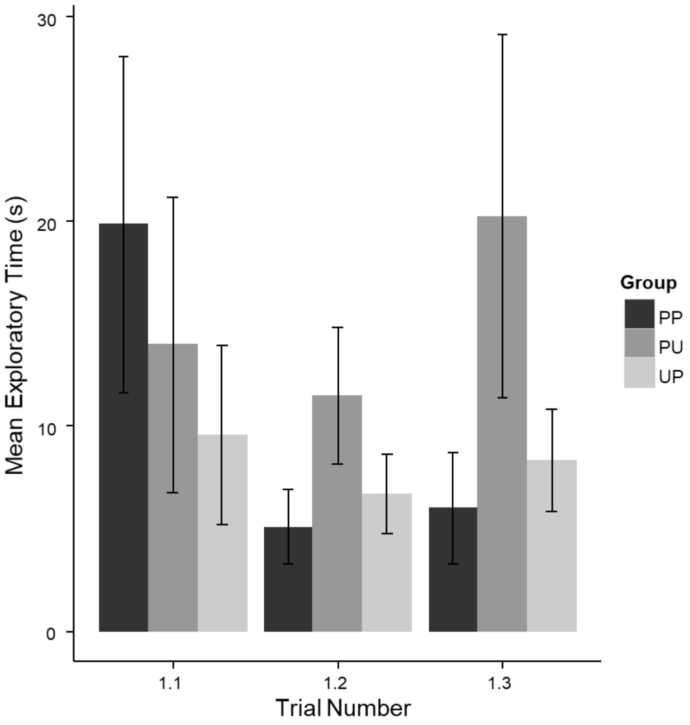

Figure 6.2 The interaction between the mean exploratory time of the US, Trial Number (1.1-1.3), and the Group individuals were assigned to in Phase **I** (N = 27). Exploration was measured as the time individuals spent exploring the area around the US (i.e. corn kernels), while group membership consisted of whether the CS1 and the US were paired (P-P, P-U) or unpaired (U-P) in Phase **I** (see legend). Mean and standard errors are shown.

In the second case, I found that exploration decreased in Trials II.2 and II.3 (Table 6.6, Fig 6.3A). Additionally, compared to the P-P Group, individuals of the U-P Group were less likely to explore the CS2, regardless of the trial (Fig. 6.3B). Lastly, I found that biting the CS2 and Group membership were significantly associated: individuals from the P-P Group bit the CS2 more than the control groups ($X^2 = 6.37$, $p = 0.04$). However, this was not the case for sniffing behavior in the same Phase, nor biting and sniffing in Phase III ($p > 0.05$).

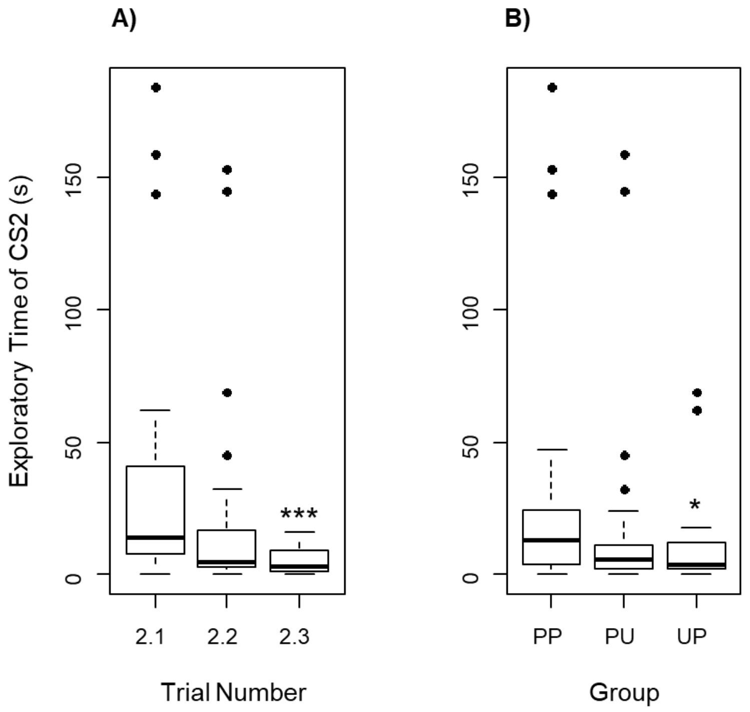

Figure 6.3 The relationship between: (**A**) exploratory time of the CS2 and Trial Number (II.1-II.3) in Phase II; and (**B**) exploratory time of the CS2 and Group membership in Phase II (N = 27). Exploratory time of the CS2 was measured as the time individuals spent exploring blue square including handling, sniffing or biting, while Group membership consisted on whether the CS1 and the CS2 were paired (P-P, U-P) or unpaired (P-U) in Phase II. On each box, the bold line represents the median of the distribution, while the bottom and top represent the 25th and 75th quartiles respectively. Significance is represented by * (*p* = <0.05) or *** (*p* = <0.001).

6.5 DISCUSSION

I tested whether wild baboons could learn novel associations through a second-order conditioning task. I failed to find evidence that individuals in the experimental group successfully associated novel cues through second-order conditioning. This is perhaps unsurprising given that I found little evidence that the baboons could make a first-order association. Below, I discuss three factors that could have prevented such an association being formed, namely: (1) the timing of the presentations within trials in Phase I; (2) the number of trials needed to succeed at second-order conditioning; and (3) the extinction of the conditioned response. Additionally, I discuss the biological significance of being able form second-order associations in the wild.

Studies on Pavlovian conditioning observe that the timing of events, in particular the temporal intervals between the CS and US, determine the emergence of the conditioned response (Kirkpatrick & Balsam, 2016; Ward-Robinson, 2004). Successful conditioning may depend not only on the time contiguity between the US and CS, but also on whether the CS is presented before or after the US. Individuals are more likely to learn to associate the US with the CS if the CS precedes the US (Kirkpatrick & Balsam, 2016). However, many studies are unclear about the order that stimuli are presented in their experiments (e.g. *Carassius auratus:* Amiro & Bitterman, 1980; *Cotournix japanica:* Crawford & Domjan, 1995; *Drosophila melanogaster:* Tabone & de Belle, 2011). In this experiment, the stimuli were presented simultaneously. Given the possible importance of a brief delay between the presentations of the CS1 and US, the lack of such a delay in this experiment might explain why the baboons failed to make an association. However, while second-order conditioning can still be accomplished when the CS1 and CS2 are presented simultaneously (Rescorla, 1982), an interval between the CS and US may well be necessary to ensure animals attend to each stimuli distinctively and learn the relation between them.

I expected that in Phase I, the P-P and P-U Groups would show a greater CR response (i.e. greater exploration of the area around the US) than the U-P Group; however, while this was true for the P-U Group, the P-P Group did not. Moreover, individuals from the P-P Group had shorter exploratory times than members of the U-P Group after the first trial. Successful conditioning may be determined by attributes of the CS, such as its duration (Holland, 1980). A short CS, for instance, can be unnoticed by animals who will then be unable to exhibit the conditioned response later on (Kirkpatrick & Balsam, 2016). However, I explicitly tested whether the exposure time and vigilance during the trials affected the exploration of the CS in subsequent trials but found no evidence that this was the case. At this point, I can only speculate the reason for such differences and whether an uncontrolled variable; however, since individuals were assigned randomly to each group, the most likely explanation is that the sample sizes weren’t big enough to discern other patterns that might explain the differences observed.

In Phase II, individuals in the U-P group were less likely to explore the CS2 than members of the P-P and P-U groups. This was expected, as individuals in this group did not receive the pairing of the CS1 and UP and did not form a first-order conditioning. Additionally, by trial 3 in this Phase, all individuals had decreased their exploration of the CS2 regardless of Group membership. Another reason that second-order conditioning was not achieved could be because the baboons quickly learnt CS2 did not involve any food rewards. In classical conditioning theory, when a CS ceases to be reinforced, that is, when the CS is not followed by the US, the conditioned response becomes extinct (Castro & Wasserman, 2010). In second-order conditioning, extinction is observed when the unreinforced presentation of the CS1 causes the response to the CS2 to disappear, which should eventually occur in Phases II and III. Extinction of the CR may additionally depend on other aspects of the conditioning process, such as the duration of the CS1 (Holland, 1980) or the temporal relation between the CS1 and the CS2 (Rescorla, 1982). Rescorla (pigeons: 1982) for instance, found over a series of experiments with rats, that the response in second-order conditioning was sensitive to the extinction of the CS1 when it was simultaneously paired with the CS2 but not when it was serially paired, while other studies have successfully generated second order conditioning responses even when the CS1 is simultaneously paired with the CS2 (e.g. fruit fly: Tabone & de Belle, 2011). A possible explanation for why the response to the CS2 became extinct faster in the U-P Group in Phase II, may be because the U-P Group did not experience a paired CS1 and US in the previous Phase; therefore, their exploration of the CS2 decreased faster across trials compared to the other two groups that did experience the pairing simultaneously. A similar conclusion can be made with regards to the decrease in exploration observed across trials in Phase II. Exploration of a novel object is used to acquire information that can potentially be exploited (e.g. food: Biondi et al., 2010); however, since our CS2 offered no reward, it is not surprising that individuals reduced their exploratory time after a single trial, regardless of the Group they were in. Perhaps animals that live in highly variable environments such as the baboons tested here, sample stimuli frequently, but do not persist for long periods when exploration is unrewarded.

The inter-trial interval (ITI), like the temporal contiguity between the CS and US, has similarly been observed to affect conditioning, as learning is related to the time between trials (Sunsay & Bouton, 2008). One of the possible reasons for why ITIs are important has to do with the role of contextual or background cues that are present at the time of testing. Such cues can become the *de facto* CS, as individuals learn to associate US presentations with the context rather than the stimulus (Marlin, 1983). For instance, Marlin (1983), reported mice avoided licking a water tube when hearing a tone that had been previously associated with an electric shock in one of two auditory contexts (i.e. white noise in the background vs no noise). Having longer ITIs can cause the extinction of contextual cues and avoid such associations (Sunsay & Bouton, 2008). Second-order conditioning experiments commonly have short ITIs (range: 30-600 s) (Crawford & Domjan, 1995; Jennings & Kirkpatrick, 2018; Ward-Robinson, 2004) yet it is impossible to tell whether uncontrolled contextual cues might have had an effect conditioning with ITIs of such length, even when, the background context is presumably consistent in captivity. Compared with our experiment, where the average ITI was approx. 3600 s, the longest ITIs recorded in captive settings were 1800 s (1,920 s: Sunsay & Bouton, 2008). Since the animals we evaluated were unrestricted in their movement, and tested throughout the day, it is safe to assume contextual cues in each trial were never the same; therefore, it seems unlikely that having a long ITI would reinforce the CS1-US /CS2-CS1 associations. Studies report longer ITIs (range: 12-1,960 s) produce a stronger conditioned response (e.g. Holland, 1980; Lattal, 1999; Sunsay & Bouton, 2008); however,, it could be possible that the ITIs in our experiment were too long for individuals to form an association in the first place due to lack of continuous reinforcement within shorter periods of time. Although the length of the ITIs likely constrained the formation of second-order associations, they may be more representative of the normal encounter rates of stimuli in wild conditions.

Conditions in captivity may provide an ideal scenario for development of second-order conditioning; however, they may be difficult to recreate in wild settings. In addition to having relatively short ITIs, the majority of second-order conditioning studies have a large number of trials in each phase of testing. Previous studies that have demonstrated second-order conditioning do so after testing each animal over several sessions, with each session consisting of multiple trials (e.g. Amiro & Bitterman, 1980; Crawford & Domjan, 1995; Rescorla, 1982). Testing animals repeatedly remains one of the challenges of testing animals in the wild and is likely one of the reasons why second-order conditioning has not yet been tested in wild conditions. Whether differences in the number of trials in second-order conditioning affects the occurrence of a response and its consolidation has so far, not been explored as animals have either been tested until reaching a criterion of success or tested over set number of trials per phase. While I tested each baboon with a set number of trials in each phase, this number is usually higher than what is possible to do in the wild. The typical study in captivity would use 10-20 trials in each phase (goldfish: Amiro & Bitterman, 1980; rats: Holland, 2000), although some captive studies have achieved second-order conditioning with as few as 5 trials per phase (Japanse quails: Crawford & Domjan, 1995). It is possible that the 3 trials per phase used in this study was an insufficient number to establish CS1-US/CS2-CS1 associations.

Was the baboons’ failure to achieve second-order conditioning because appropriate cues were not used? It is not uncommon for studies testing first- and second-order conditioning to use auditory cues, such as the clicker used here (Balsam & Gallistel, 2009; Holland & Rescorla, 1975), paired with a visual stimulus (Crawford & Domjan, 1995; Hall & Suboski, 1995; Hussaini et al., 2007). More recently, experiments have expanded to the use of olfactory (Hall & Suboski, 1995; Tabone & de Belle, 2011), background context (Marlin, 1983) and even social cues (Dawson et al., 2013) to elicit a second-order response. Chacma baboons are capable of learning and recognizing auditory cues such as calls from conspecifics, particularly those of their kin, and respond accordingly (e.g. by providing coalitionary support) (Cheney & Seyfarth, 2007; Engh et al., 2006). Additionally, baboons commonly use visual cues to quickly identify threatening stimuli, such as heterospecific threats (Carter et al., 2012), and can similarly produce auditory cues (i.e. alarm calls) on which conspecifics act. Gregarious animals such as baboons often rely on social information to exploit new resources (Thornton, 2008); consequently, it is possible that in order to make second-order associations, gregarious animals prioritize social cues, whether visual, auditory or olfactory, as their perceptual system is already adapted to respond to them (Dawson et al., 2013). A study with bumblebees (*Bombus terrestris*: Dawson et al., 2013) reported such results, as individuals observed demonstrators to form second-order associations involving colour cues. It’s possible that to make second-order associations baboons attend to other cues from their environment, conspecifics or a combination of both.

One of the limiting aspects of second-order conditioning testing is that, so far, all experiments have been carried out in captive settings. This raises the question of whether animals make second-order associations in the wild as readily as in captivity. While second-order associations facilitate learning new associations based on previous first-order responses, it may also require stimuli to be consistent through time with comparable intensity. The environment in which the baboons under study live is characterized by strong seasonal shifts (Hamilton, 1986), where the availability and distribution of foraging resources changes throughout the year (Guy Cowlishaw & Davies, 1997). Moreover, when this experiment was conducted in 2016, Namibia was suffering an extreme drought period (refer to Chapter 3 for more details) that affected the presence of resources in that time of year. As such, it is possible the ability and need of second-order conditioning is more likely to develop in stable environments, where animals are exposed to consistent cues that produce a conditioned response. If we aim to understand whether and how animals are capable of making second-order associations, testing animals in the wild could provide us with an ecological and evolutionary context in which such abilities potentially develop.

To the best of our knowledge, this is the first second-order conditioning experiment conducted under wild conditions. I have discussed above the challenges involved in testing animals in their environment, including the difficulty of testing animals multiple times over an appropriate time period; having a sufficient sample size of individuals and trials; and being limited by methodological challenges of testing wild animals. These points can apply to a number of species but are a particular challenge in tests involving large mammals. My work is very much experimental; however, I consider it a first step towards developing *in situ* tests that have historically been used exclusively in captive conditions. My work demonstrates the limitations of captive tests in predicting the behaviour of wild animals. Although I failed to find evidence of second-order conditioning, I cannot rule out wild baboons are capable of making second order associations; rather, the results described here may reflect the methodological constraints common in studies in wild settings. Work like the one presented here can provide us insight into the sort of cues wild animals respond to and the temporal patterns required to produce a response. Future studies, particularly those in captivity, should aim to evaluate second-order conditioning using ecologically relevant cues as well as a temporal contiguity that resembles what would be possible in the wild.

Chapter 7

Differences In Task Participation In A Group Of Wild Chacma Baboons

7.1 ABSTRACT

In spite of the controlled testing conditions that are typical of captive environments, many cognitive evaluations fail to ensure all individuals participate. This even more evident in cognitive studies in wild conditions, as animals are not restricted or isolated and have other activities available. Two behavioural aspects are commonly attributed to determine participation: motivation and responses to novelty (i.e. neophobia); however, even when these are controlled for through food rewards and habituation, respectively, animals still fail to participate in tasks, either by not approaching the task or, if they approach, by not engaging with the task (i.e. manipulation of the task). In this chapter, I investigate the variation found in a group of wild chacma baboons (*Papio ursinus*) to approach and explore two tasks: an associative learning task and a second-order conditioning task. At the same time, I explore the relationship of three variables and their associated phenotypic traits/states with the motivation to participate, based on the latency and likelihood to approach the task and the subsequent exploration given to the stimuli: (1) the availability of competing activities; (2) the opportunities to exploit information (i.e. producer-scrounger model); and (3) stressors experienced immediately prior to

testing. I find consistent results in both tasks regarding the effect of age both independently, and in relation with competing activities and information use opportunities. Differences in information use in particular determine much of individuals’ motivation to participate relative to the phenotype and/or state of individuals and the stage of the task. Nevertheless, there are still some questions, particularly concerning the differences found between each task, as well as the role the current environment plays in individuals’ participation.

7.2 INTRODUCTION

Cognitive assessments in animals have historically been restricted to captivity, as it offers an controlled environment where external variables that could affect task performance are minimised (van Horik et al., 2016). Nevertheless, even in such conditions a significant number of studies fail to achieve the full participation of all individuals involved. Moreover, although the likelihood of success is dependent on participation, studies often fail to report the number of non-participants in a given assessment (e.g. *Parus major*: Cauchard et al., 2013; *Poecilia reticulata:* Trompf & Brown, 2014). For instance, Cole et al. (2011) reported that 44% of 570 great tits (*Parus major*) solved a lever pulling task but it is unclear whether “non-solvers” attempted the task unsuccessfully or failed to interact with the task at all. Moreover, participation is not solely limited to task engagement but requires an initial approach to the task (e.g. Gajdon et al., 2004; Thornton & Samson, 2012). Krasheninnikova & Schneider (2014), for instance, reported that only 10 of 23 orange-winged amazons (*Amazona amazonica*) entered a test room before 5 of these 10 individuals could successfully complete a string-pulling task. Perhaps unsurprisingly, lack of participation is even more common in wild conditions, as animals cannot be completely isolated from other activities that compete with the task or easily motivated via food rewards or food/water deprivation prior to engaging with the task (e.g. *Papio ursinus:* Laidre, 2008; *Suricata suricatta:* Thornton & Samson, 2012; *Chlorocebus aethiops*: van de Waal et al., 2010). Table 7.1 provides an overview of participation patterns in cognitive assessments, including how studies promote participation in each task and the experimental setting in which the assessments are carried out.

Table 7.1 Differences in participation and the assessments of novelty and motivational responses.

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
Aplin et al., 2013	Great tits *Parus major*	Wild-caught	Social learning task	91 out of 95 individuals participated	NEOPHOBIA: latency to approach the apparatus	Food rewards used during testing (i.e. food motivation); body condition
Ashton et al., 2018	Australian magpie *Cracticus tibicen dorsalis*	Free-ranging	Inhibitory control; associative and reversal learning; and spatial memory tasks	46 out of 56 individuals participated in all tasks: 56 inhibitory control task; 48 in the associative and reversal learning tasks; and 49 in the spatial memory tasks	NEOPHOBIA: time elapsed between individual coming 5m of the apparatus, and first contact with it	Food rewards used during testing (i.e. food motivation)
Biondi et al., 2010	Chimago Caracara *Milvago chimago*	Wild-caught	Problem-solving task	15 out of 18 participants touched and handled at least on object in the exploration test; all individuals approach the food in the neophobia test; all individuals approached the problem solving-task in the control session	Habituation to captive conditions NEOPHOBIA: latency to feed in trials with a novel object next to food EXPLORATION: latency time to approach three novel objects; contact latency; number of objects contacted; and total exploration time	Individuals tested in isolation to avoid social motivation (i.e. scrounging); food rewards used in each trial (i.e. food motivation)
Boogert et al., 2006	Starlings *Sturnus vulgaris*	Wild-caught	Extractive foraging task	15 out of 15 individuals interacted with the apparatus	Habituation to the apparatus	Food rewards used during neophobia test

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
					NEOPHOBIA: neophobia test; latency to feed in a novel environment; latency to feed near a novel object	and in each trial (i.e. food motivation)
Boose et al., 2013	Bonobos *Pan paniscus*	Captive	Extractive foraging task	2 out of 14 individuals never interacted with the apparatus during observation time; 7 out of 14 did not interact with the apparatus in their first trial	Habituation to the apparatus	Food rewards used during testing (i.e. food motivation)
Cauchoix et al., 2017	Great tits *Parus major*	Free-ranging and wild-caught	Reversal learning task	34 out of 54 wild individuals; 29 out of 29 captive individuals. MEASURED: logged on the device's antenna. 33 out of 34 wild individuals; 29 out of 29 captive individuals. MEASURED: pecking of the key at least once. 20 out of 34 wild individuals, 17 out of 29 captive individuals. MEASURE: complete 1st reversal training	Habituation to captive conditions; shaping with a dummy operant box for captive animals	Testing preceded by food deprivation

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
Cronin et al., 2014	Chimpanzees *Pan troglodytes*	Captive	Problem solving task	1 out of 15 individuals did not participate in all possible sessions; differences in task participation during training	Habituation to captive conditions and the device	No food or water deprivation; order of sessions were not predetermined.
Dean et al., 2011	Ruffed Lemurs *Varecia variegata* & *Varecia rubra*	Captive	Innovation tasks	38 out of 43 individuals contacted at least one of the 3 tasks presented; 33 out of 43 manipulated at least one task; 23 out of 43 solved at least one task.		Food rewards used in each trial (i.e. food motivation); no food deprivation before testing
Fagot & Bonté, 2010	Guinea baboons *Papio papio*	Captive	Alternative-forced choice; matching-to-sample tasks; individuals received training beforehand	20 out of 26 individuals in 2 experiments (6 were left out due to sickness or age). 12 out of 20 in a 3rd experiment.	Habituation to the device	No food deprivation. MEASURED: high levels of participation (298-774 trials); rewards were provided
Fagot & Paleressompoulle, 2009	Guinea baboons *Papio papio*	Captive	Motor control; abstract reasoning tasks; individuals received training beforehand	7 out of 8 individuals; participation inhibited by high-ranking conspecific.	Habituation to the device	No food deprivation. MEASURED: high levels of participation (95-112,729 trials); rewards were provided
Franks & Thorogood, 2018	Hihi *Notiomystis cincta*	Free-ranging	Associative learning task	78 out of 97 individuals visited the apparatus; 59 did not participate in the first stage of testing; 12 did not	Habituation to the general characteristics of the apparatus	Food rewards used in each trial (i.e. food motivation)

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
				participate in the second stage of testing.		
Gajdon et al., 2004	Kea *Nestor notabilis*	Free-ranging	Problem-solving task; social learning	5 out of a maximum of 15 individuals approached the apparatus in both, the baseline and test phases.		Food rewards used during testing (i.e. food motivation)
Isden et al., 2013	Spotted-bowerbirds *Ptilonorhynchus maculatus*	Free-ranging	Barrier removal; novel motor; colour discrimination; color reversal; shape discrimination; spatial memory tasks	11 out of 19 individuals participated in all tasks; 5 failed to participate in all tasks; 3 in at least 1.		Food rewards used during training and in each trial (i.e. food motivation) MEASURED: time taken to move objects more than 20 cm away (barrier removal task); presenting a rewarded well with no colour cues
Krasheninnikova & Schneider, 2014	Orange-winged amazon, *Amazona amazonica*	Captive	Problem-solving string tasks	Tested individually: 10 out of 23 individuals entered test room; 7 out of 23 participated in the task; 5 out of 23 completed the task. Tested socially: 15 out of 35 participated in the task; 12 out of 35 completed the task	NEOPHOBIA: latency to feed from a novel feeder; latency until first contact with the string of the first task	Food rewards used during testing (i.e. food motivation)

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
Laidre, 2008	Chacma baboons *Papio ursinus*	Free-ranging	Innovative food-access tasks	7 out of 62 individuals that approached the tasks interacted with them in the first day of testing; 1 out of 62 individuals that approached the tasks interacted with them in the last day of testing. Experiments ended if the individual failed to come within 5m of the apparatus for 10 min		Food rewards used during testing (i.e. food motivation)
Mirville et al., 2016	Australian magpie *Cracticus tibicen dorsalis*	Free-ranging	Associative learning task	28 out of 34 individuals made contact with the task; 18 out of 34 flipped at least three lids on the grid MEASURED: individuals were considered participants if they approached and made contact with the foraging grid		Food rewards used during testing (i.e. food motivation); food was visible during shaping but not during testing
Morand-Ferron et al., 2015	Greta tits *Parus major* Blue tits *Cyanistes caeruleus* Coal tits *Periparus ater* Marsh tits *Poecile palustris*	Free-ranging	Associative learning task	144 out of 2832 individuals visited the apparatus, of which: 88 were great tits; 43 blue tits; 3 were coal tits; and 10 were marsh tits. 80 out of 144 pecked the key, of which 67	EXPLORATION: number and duration of flights, number of hops and areas explored during an 8 min assay in a novel environment	Food rewards used during testing (i.e. food motivation)

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
				were great tits; 8 blue tits; 4 were coal tits; and 1 were marsh tits		
Sol et al., 2012	Common myna *Sturnus tristis*	Wild-caught	Consumer and motor innovation tasks	33 out of 60 individuals in both tasks	Habituation to captive enclosure and test cages; habituation to test apparatus. NEOPHOBIA: success of individuals who ate food next to a noel object; latency to start feeding; latency to approach feeder	Overnight food deprivation prior to morning tests MEASURED: latency to approach a food dish between initial and final phases
Thornton & Samson, 2012	Meerkat *Suricata suricatta*	Free-ranging	Innovative foraging task	63 out of 135 participants MEASURED: interaction with the apparatus	No habituation NEOPHOBIA: latency to the apparatus	Food rewards used during each trial (i.e. food motivation); presentations were made early morning
Titulaer et al., 2012	Great tits *Parus major*	Wild-caught	Associative learning; behavioural flexibility	52 out of 54 individuals participated. MEASURED: individuals were considered participants if they lifted the covers from the apparatus.	EXPLORATION: time it took birds to reach 4 out of 5 trees in a novel environment; latency to approach a novel object and the	Food deprivation on the day of testing; food rewards used during each trial (i.e. food motivation); food was not visible

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
					closet distance at 120s.	
Johnson-Ulrich et al., 2018	Spotted hyena *Crocuta crocuta*	Captive	Inhibitory control; innovation	10 out of 10 participants tested individually MEASURED: trials began when individuals entered the arena and ended when the task had been solved or after 15 min.	Habituation to the test apparatus (i.e. familiarization trials) NEOPHOBIA: latency to feed from the apparatus in the first familiarization trial	MEASURED: latency from the start of the trial to first contact with the apparatus; food rewards used in each trial (i.e. food motivation)
van de Waal et al., 2010	Vervet monkeys *Chlorocebus aethiops*	Free-ranging	Social Learning; "artificial fruit"; no habituation; demonstrator training	64 out of 108 participants. MEASURED: individuals were considered participants if touched the apparatus		No food deprivation
van Horik & Madden, 2016	Pheasants *Phasianus colchicus*	Captive	Extractive foraging task: Flip-top, Flip-cup & Petri-dish	184 out of 200 participants Flip-top & Flip-cup tasks; 83 out of 100 participants in Petri dish task MEASURED: individuals were considered	No habituation.	MEASURED: Time to acquire the food-item; order in which each individual entered the testing chamber; goal directed

Authors (ordered alphabetically)	Species	Experimental Setting	Task	Participation	Novelty response	Motivation
				participants if they acquired the base worm (BW); subjects who participated in a task, likely participated in the other		control. No food deprivation
van Horik & Madden, 2016	Pheasants *Phasianus colchicus*	Captive	Novel motor skills; colour discrimination; colour reversal; shape discrimination; spatial memory tasks.	54 out of 144 participants in all possible test sessions. MEASURED: individuals interacting with the arena 120s after entering it; attempt to obtain meal-worm	Habituated and shaped to enter testing chamber. NEOPHOBIA: exploration of a novel environment; latency to approach a novel object; latency to approach an unknown conspecific	Food rewards used during shaping; food deprivation prior to testing; food reward was provided in each task; shaping with food immediately prior to test. MEASURED: order each individual entered the testing chamber; time to acquire the freely-available food-item (i.e. food motivation)
Vonk & Povinelly, 2011	Chimpanzees *Pan troglodytes*	Captive	Tool-use; gaze-following tasks.	No individual out of 7 participated in all tasks in the training and testing phases.		

Show are the details of each study, including: (*i*) the authors and year of publication; (*ii*) common and latin (in *italics*) name of the species; (*iii*) the experimental setting animals were tested in: “free-ranging” refers to wild animals that were rested in their own habitat, “wild caught” refers to wild animals tested in captivity and “captivity” refers to captive animals tested in captivity; (*iv*) the task animals were tested with; (*v*) the number of participants out of the total sample tested, including different points of participation, and whether participation was directly measured; (*vi*) whether the response to novelty was directly measured in a test and/or controlled for in any way; (*vii*) whether motivation was directly measured in the test and/or controlled for in any way.

Two attributes are commonly used to explain differences in participation: neophobia, the aversion to novel stimuli (Greenberg, 2003), and motivation, usually defined as reversible changes in state that affect behaviour (McFarland, 1991). Both attributes are commonly assessed and/or “controlled for” in cognitive tasks, either (1) experimentally, by habituating animals to the task beforehand in the case of neophobia, or by restricting food/water prior to testing and/or using appetitive tasks (i.e. food rewards) in the case of motivation; or (2) statistically, through behavioural observations which are later included as control variables in the statistical analysis (See Table 7.1 for a summary of studies that have either directly assessed or controlled for these two attributes). Nevertheless, full participation in wild conditions, either by initially approaching or subsequently engaging with a task, is less frequent. Why an animal fails to participate due to neophobia or poor motivation may reflect a variety of factors at the species and individual level, including the species’ ecological characteristics (Greenberg, 2003), seasonal changes in physiology and the environment (Greggor et al., 2016), and individuals’ phenotypic traits (e.g. body size: Laland & Reader, 1999) and states (e.g. age: Greenberg, 2003).

In recent years, the cognitive sciences have shifted their focus from between-species to within-species differences in cognitive abilities (Thornton & Lukas, 2012). Identifying potential causes for such differences should invariably include differences in participation, as our understanding of individuals’ cognitive abilities, as well as those of a species, may be biased towards those individuals that fully participate (i.e. sample bias: Carter et al., 2012; van Horik et al., 2016). The aim of this study was to evaluate within-and between-individual differences chacma baboons' motivation to participate in two cognitive tasks in the wild. I focussed specifically on motivation because in the years in which baboons were tested, there was an ongoing drought that severely limited the availability and distribution of resources, likely making individuals' responses more strongly driven by their motivational states than by any neophobia. Three factors that may explain the observed variation in task participation are (1) competing activities at the time of testing, (2) the opportunities individuals have to exploit information, and (3) immediate stressors prior to testing. These factors may affect animals in captive and wild conditions but will likely affect task participation in wild animals more, as testing conditions are usually more extreme and more difficult to control. I address each of these in turn.

1. Competing Activities At The Time Of Testing

Competing activities are a particular challenge for testing under wild conditions. Unlike in captivity, where animals are tested in isolation (e.g. van Horik et al., 2016) and the opportunities and needs for other activities are reduced, testing in the wild often requires animals to choose between investing time and energy in a task or in participating in other activities, such as foraging (Cauchoix et al., 2017). Automated testing, which allows individuals to participate voluntarily, has provided some insight into when test subjects might favour task participation over competing activities. For example, Fagot & Bonté (2010) reported that captive guinea baboons (*Papio papio*) preferred interacting with an automated device over objects provided for enrichment and rest, likely because the apparatus offered a food reward. Nevertheless, in any setting (i.e. captive or wild), but particularly in the wild, some activities may be preferred by individuals when given the choice, as they may offer benefits that are not necessarily substituted by interacting with a task, for instance socializing or foraging on preferred foods.

2. Information Use Opportunities

Individuals can gather information about their environment in two ways: (1) by directly collecting information from it and (2) by using the information conspecifics collect (Giraldeau & Caraco, 2000). Within a social group, individuals may typically differ in their use of information depending on their phenotype: some phenotypes may have a greater propensity to generate social information (i.e. information producers), while others are more likely to exploit it (i.e. information scroungers) (Giraldeau & Caraco, 2000, but see: Carter et al., 2015). Whether an animal is more likely to generate or exploit social information may depend on their opportunity to do so, based for example, on their phenotypic traits (Lee et al., 2016) or states (Aplin & Morand-Ferron, 2017). For instance, shy barnacle geese (*Branta leucopsis*) scrounge more from conspecifics, because they are less active than bold conspecifics and have more time to be social (Kurvers et al., 2010). The extent to which animals generate or exploit may influence their motivation to participate in tasks, as individuals who have a greater opportunity to use social information may feel less need to approach and explore novel stimuli on their own.

3. Immediate Stressors

In animals, as in humans, stressors can have negative and positive effects on cognition (Joëls et al., 2006). For instance, a short term-stressor can lead to an adaptive change, whereas a long-term stressor often causes detrimental changes in cognitive abilities

(Luine et al., 2007). Stress responses have long been thought to account for differences in task participation in both captive and wild conditions. In captivity, for instance, lack of participation is mostly attributed to two stressors: (1) the stress of separation from conspecifics when tested in isolation (Cauchoix et al., 2017); or (2) the stress of intimidation and/or aggression due to the inescapably close proximity of conspecifics when tested in a social setting (Maestripieri et al., 1992). Wild animals may experience similar social stressors, such as frequent aggressive interactions, but also environmental stressors, such as such as differences in food availability (i.e. nutritional stress: Pritchard et al., 2016) or the presence of predators (Beehner & Bergman, 2017). Nevertheless, it remains unclear whether differences in participation occur in response to immediate stressors (e.g. short-term aggressive events experienced prior to testing) or to long-term stressors as a result of an individuals' phenotype or state (e.g. social rank).

In this chapter, I explore variation in task engagement with two cognitive challenges in wild chacma baboons. I begin by assessing the motivation to participate, quantified as both, the likelihood and latency to contact each task and the degree of exploration of the task after contact. I chose these measures because they represented two distinct stages at which motivational differences could have determined success in both tasks. I then test four hypotheses, that (**H1**) competing activities affect the motivation to participate, (**H2**) individuals who are more likely to use personal information due to a lack of opportunities to exploit social information, will be more motivated to participate, (**H3**) immediate stressors will affect individuals' motivation to participate, and (**H4**) the motivation to participate will be influenced by individuals' phenotypic traits and/or states, namely, sex, age, social rank and personality. I included personality to ensure differences in participation truly represented motivational differences and not a response to novelty. Personality, which is measured according to fast-slow behavioural types (Sih & Del Giudice, 2012), is an important determinant of task participation (Carere & Locurto, 2011) and has previously been linked to the variables assessed here, such as social information use preferences (Kurvers et al., 2010). This study was conceived from the behavioural observations made while testing individuals with each cognitive task. As such, the hypotheses listed in Table 7.2, are based on postdictions.

Table 7.2 Postdictions in the assessment of individual differences in participation in an associative learning and second-order conditioning tasks.

	Hypothesis	Participation postdiction
Competing activities	H1	Individuals engaged in high-quality activities, namely foraging and grooming, will be: (1) less likely/have longer latencies to contact a task; and (2) dedicate less exploratory time than those who were not so engaged.
Information Use	H2	Individuals who have a greater opportunity to exploit social information more frequently, i.e., information scroungers, will (1) be less likely/have longer latencies to contact a task; and (2) have shorter exploratory times as they are commonly less likely to approach and explore novel situations on their own compared to information producers.
Immediate Stressors	H3	Individuals who were recently the recipients of aggression from other troop members or exhibited a higher rate of self-directed prior to testing, will: (1) be more likely/have shorter latency times to contact the task; and (2) have a longer exploratory time of the task. This is because the motivation to

	Hypothesis	Participation postdiction
		approach novelty may be an adaptive response to acute stressors.
Sex	H4	Males will be motivated to approach a task, as they might be hungrier due to their larger size, which is costly to maintain (Key & Ross, 1999).
Age	H4	Juveniles will be more motivated to participate in cognitive tasks as they are more likely to explore novel stimuli to acquire information and experience (Galef & Laland, 2005).
Social Rank	H4	There are two possibilities regarding social rank: (1) Low-ranking animals will be more motivated to participate in cognitive task as are normally restricted in their access to resources by their dominant conspecifics (i.e. they may be hungry: Laland & Reader, 1999); or (2) low-ranking animals will be less motivated for fear of aggression from higher ranking conspecifics (Drea & Wallen, 1999).
Personality‡	H4	Bolder animals will be more likely to participate in cognitive tasks than shy conspecifics as they are more likely to approach and explore novelty (Sih & Del Giudice, 2012).

Shown are the postdictions regarding the effects of competing activities (H1), information use opportunities (H2), immediate stressors (H3), and individuals' phenotypic traits (sex, social rank, personality) and states (age) (H4) on both the latency to approach the task and the degree of exploration given to it. The prediction for personality, marked here with a double cross (‡), is based on the response to novelty rather than motivation

7.3 MATERIALS & METHODS

7.3.1 Study Site And Species

This study was carried out over two field seasons of six and five month duration over two years (April-September 2015; May-September 2016) on two fully-habituated troops (J and L Troops) of wild chacma baboons at the Tsaobis Baboon Project, Tsaobis Nature Park (15° 45’E, 22° 23’S), on the edge of the Namib Desert, Namibia. Chacma baboons were chosen as a model species for this work because, as a robust terrestrial primate species, they are tractable for field experiments and their social and physical environment can be easily quantified. For more information on this species and the two study troops please refer to Chapter 3.

7.3.2 Experimental Protocol

I previously tested two groups of baboons with two cognitive tasks, each of which consisted of presenting individuals with a novel stimulus: (1) an extractive foraging task, which tested the ability of individuals to associate a visual stimulus with a food reward; and (2) a second-order conditioning task, which evaluated the ability of individuals to make sequential associations. Both tasks were considered for this Chapter as there were quantifiable differences in individuals’ level of participation regarding their latency/likelihood to contact a stimulus and exploratory behaviour. In comparison, a third task which presented a food reward, saw the full participation of all individuals tested.

Extractive foraging task

A representative sample of 37 baboons was tested with a novel extractive foraging task over the months of July-September 2015. The task involved two coloured paper bags (i.e. red and green) which differed in value: one with corn kernels inside (i.e. a food reward) and the other with small rocks (i.e. no reward). Each individual was assessed three times with a three-day interval between each presentation (mean; median re-test interval: 3.14; 3.00 days). See Chapter 3 for further details on the test sample, and Chapter 5 for a full description of this task.

Second-order conditioning

A representative sample of 27 baboons was tested with a second-order conditioning (SOC) task over the months of June-September 2016. The task involved conditioning individuals over series of presentations using the pairings of corn kernels with a clicker and a blue cardboard square with a clicker. Each individual was tested on nine separate occasions in three phases over the course of a single day. Each phase involved three presentations with an average inter-trial interval of 57 min (range 20-227 min), such that a full assessment lasted about nine hours in total. See Chapter 3 for further details on the test sample, and Chapter 6 for a full description of this task.

7.3.3 General Protocol

Observers followed both groups of baboons on foot from dawn to dusk. All individuals over four years of age were individually identifiable. Observers moved throughout the troop, using the freely available software Cybertracker (www.cybertracker.org) on individual smart phones (Samsung Galaxy S4, Samsung, Seoul, South Korea) to record dominance and social interactions *ad libitum*. In addition, focal observations were collected on all identifiable individuals tested in both cognitive tasks (see below). These focal follows were carried out throughout both field seasons (2015-2016) in order to collect data describing individuals' foraging patterns and aggressive/affiliative interactions. Focal observations lasted between 20 and 30 min (any observation less than 20 min was discarded), and no individual was focal followed more than once per day. Study subjects tested in 2015 alone (n = 22) were observed for a maximum of 4 h across two 30 min focal observations in each of four time periods (0600-0900, 0900-1200, 1200-1500 and 1500-1800 h) generating a median of 4 h per focal individual per month. Study subjects tested in both 2015 and 2016 (n = 15) were observed for a maximum of 1 h across two 30 min focal observations in each of the four time periods in each month of study, generating a median of 4 h in each field season respectively per focal individual per month. Those individuals that were tested only in 2016 (n = 12) were observed for a maximum of 30 min in each time period in every month of study (with the exception of three animals, which could not be observed for one month), generating a median average of 1 h per focal individual per month. In total, each baboon tested was observed a median average of 14 h (range: 8-14 h) and 11.5 h (range: 3.5-15.5 h) per season for the 2015 and 2016 field seasons respectively. During each focal follow all aggressive/affiliative interactions, and the activities of the focal individual including its foraging behaviour, were recorded. See Appendix S1, Table S1.3 for the ethogram used in the focal observations.

Competing activities

Although my protocol aimed to test individuals when engaged in the same initial activity (i.e. when travelling between food patches), this was not always possible as occasionally individuals became involved in a new activity right before noticing the stimuli. Therefore, in each trial, I recorded those activities in which study subjects were involved when testing began (i.e. once they saw the task). Here, I classified individuals as either engaged in a high-value activity at the time of testing (1, yes), i.e. when they were involved in foraging, drinking or grooming with a conspecific, or not (0, no) when they were engaged in a low-value activity, i.e. resting or travelling. Activities were defined as high versus low value according to the likely fitness benefits of such activities at the time of testing. Since the field site was currently going through an intense drought (refer to Chapter 3) at the time of testing, feeding would have been a priority for the baboons. Similarly, grooming interactions are an important part of baboon social life as they strengthen social bonds (Cheney & Seyfarth, 2007) and promote foraging tolerance (Marshall et al., 2015). In contrast, resting and travelling were considered low value activities because the former can be considered 'spare' time (Dunbar, 1992) and the latter primarily serves to facilitate high value activities such as feeding and grooming.

Information use opportunities

Following a similar approach to that developed in the social foraging "producer-scrounger" literature (Giraldeau & Caraco, 2000), I classified individuals' use of information along a spectrum of information 'producers' or 'scroungers'. I evaluated individuals' "scrounging behaviour" for each field season respectively, by recording the number of times the focal individual joined an occupied or unoccupied food patch during focal follows (see: Giraldeau & Dubois, 2008). Refer to Appendix S4, Table S4.1 for details on how patch occupation was evaluated. The scrounging rate (numeric, 0-1) was then calculated as the number of patch entries in which the focal animal scrounged information (i.e. the patch was occupied) divided by its total number of patch entries.

Immediate stressors

To measure each individual's motivational response to immediate stressors, I exclusively conducted 30 min focal follows (median: 1800 s, range: 600-1800) prior to every task presentation in the second-order conditioning evaluation. These focals followed the same protocol as the one described for the daily focal observations (see "General Protocol"). In total, each individual was followed nine times throughout the day at hour-long intervals on the day they were tested, albeit only six focals per individual are used here as they represent those observations done before the presentation of the blue cardboard square. Task presentation was made immediately after a focal finished; however, in cases where this was impossible, presentations occurred at the next possible chance (median interval between end of focal and presentation: 13 min, range 1-49, n=27 individuals). Stress responses were assessed with two measurements. First, the frequency of high-risk (i.e. attacks, chases, threats) and low-risk (i.e. displacements, supplants) aggression received during the focal follows, assuming that those individuals who receive more aggression will be more stressed at the start of a trial (Fitchett et al., 2005). High-risk aggression was defined as any aggressive encounter that increased the chances of or resulted in physical contact; low-risk aggression was designated as those instances in which physical contact was unlikely. Second, the rate of self-directed behaviours such as self-scratching, self-grooming or self-touching. Such self-directed behaviours are considered indicators of low-levels of stress and anxiety in non-human primates (Higham et al., 2009; Maestripieri et al., 1992). See Appendix S1, Table S1.1 for the description of aggressive and self-directed behaviours.

Individual differences

For all individuals, I classified the sex, rank, and personality as phenotypic traits and age class as a state. For details on how each variable was measured please refer to Chapter 3. Age was established in 2015 and re-assessed the following year to account for changes to adulthood in males and females. Personality scores were assessed in 2015 and again in 2016; however, between years there was no significant change between these scores so only the 2015 ones were used.

7.3.4 Statistical Analysis

I evaluated two measures of motivation for both tasks in relation to my four questions: (1) the latency to the stimulus, measured as the time between first seeing the task and contacting it; and (2) the exploratory time dedicated to the task after contacting it, measured as the time individuals spent in continuous contact with the task, including biting, sniffing and statically holding it (i.e. holding it but not actively exploring it). For the SOC task, I focussed only on the six later presentations involving the blue square, as all individuals readily approached the food stimulus in the initial three presentations (median latency = 2 s). Below I describe the general structure of the models (i.e. the predictor variables used) relative to each of the four questions of interest. I then elaborate in separate subsections how each model was fitted according to each of the response variables (i.e. latency and exploration). All analyses were conducted in the R environment (version 3.2.3, 2015).

To evaluate the effect that competing activities, information use opportunities and immediate stressors had on the likelihood/latency to contact the task and its subsequent exploration, I fitted a suite of models for the extractive foraging and SOC tasks. In the former task, the analysis consisted of two main models for each response variable, respectively using the following predictor variables: (1) a binomial variable describing whether individuals were involved in a high-value activity at the time of testing (0/1); and (2) a numerical variable (0-1) representing the scrounging rate of each individual. In the SOC task, equivalent models were fitted to the data plus a third model for each response variable that included four numeric predictor variables (0-1) describing: the rates of high-risk aggression, low-risk aggression, self-scratching and self-grooming. Self-touching behaviours were excluded from analysis, as there were only 25 instances across all focal observations (mean average of 0.15 instances per individual). A model containing the four phenotypic traits/states (i.e. sex, age class, social rank and personality) as covariates was also fitted for both response variables in each task to evaluate the effect of such traits independently. Additionally, to investigate whether the effects of competing activities, information preferences and immediate stressors varied according to individual phenotype (trait/state), I also included in each model the four phenotypic traits/states (i.e. sex, age class, social rank and personality) and their interactions with the fixed effects of interest (i.e. competing activity, information use, and stress).

This approach generated a total of 14 statistical models: six for the extractive foraging task (three each for the ‘likelihood/latency to approach’ and ‘exploratory time’ response variables), and eight for the SOC task (four each for the same two response variables). Further details of the analytical approach for the models for each response variable are given below. See Table 7.3 for a summary of the models’ design. Multiple models were required to test the competing activities, information use, immediate stress and the phenotype/state hypotheses for task participation, rather than assessing all in a single model, to avoid overparameterisation. Preliminary co-variances were assessed between the variables included in each model. If the Spearman correlation coefficients *r* between covariates were >|0.70| (See Appendix S4, Tables S4.2 & S4.3 for correlation tables between the variables for each set of models), the variable of less interest was dropped from the following analyses. The latter was determined based on the importance of each variable relative to the model being tested.

Table 7.3 Summary of model design for each of the hypotheses tested

Task	Model	Hypothesis	Response	Fixed Effects
Extractive foraging task	$\text{MLT1}_{\text{Activ}}$	H1	Latency	Activity* Sex Age Social Rank Personality
	$\text{MExT1}_{\text{Activ}}$	H1	Exploratory time	

	MLT1$_{\text{Scroung}}$	H2	Latency	Scrounging * Sex Age Social Rank Personality
	MExT1$_{\text{Scroung}}$	H2	Exploratory time	
	MLT1$_{\text{Trait}}$	H4	Latency	Sex Age Social Rank Personality
	MExT1$_{\text{Trait}}$	H4	Exploratory time	
Second-order conditioning	MLT2$_{activ}$	H1	Latency	Activity* Sex Age Social Rank Personality Trial number† Test group †
	MExT2$_{\text{Activ}}$	H1	Exploratory time	
	MLT2$_{\text{Scroung}}$	H2	Latency	Scrounging * Sex Age Social Rank Personality Trial number† Test group†
	MExT2$_{\text{Scroung}}$	H2	Exploratory time	
	MLT2$_{\text{Stress}}$	H3	Latency	High-risk Agg * Low-risk Agg* Self-scratch* Self-groom* Focal-trial interval Trial number† Test group†
	MExT2$_{\text{Stress}}$	H3	Exploratory time	
	MLT2$_{\text{Trait}}$	H4	Latency	Sex Age Social Rank Personality Trial number† Test group†
	MExT2$_{\text{Trait}}$	H4	Exploratory time	

Shown are: (*i*) the name of the task; (*ii*) the name of the model; (*iii*) the hypothesis that model is testing; (*iv*) the response variable used; and (*v*) the fixed effects used. Variables marked with an asterisk (*) indicate interactions between that fixed effect and the phenotypic traits and states listed underneath. Variables marked with a cross (†) indicate controlled effects.

Likelihood/latency to contact the stimulus

To evaluate the likelihood/latency to contact the task, I fitted a series of Cox proportional hazard models using the “survival” package (Therneau & Lumley, 2014). Survival models, such as Cox proportional hazards regression, are used in time-to-event data analyses (Jahn-Eimermacher et al., 2011) as they permit ceiling values to be included as censored data points in those cases where individuals did not approach a task (Dean et al., 2011). With the likelihood/latency to make contact as the response variable in the associative learning and SOC tasks, I fitted a suite of models evaluating the influence of: (1) the interaction between competing activities and phenotype/state (models, $\text{MLT1}_{\text{Activ}}$; $\text{MLT2}_{\text{activ,}}$ where MLT indicates a Model for Latency to approach the Task, 1 and 2 indicates the associative learning and SOC tasks, and the subscript indicates the model focus); (2) the interaction between scrounging behaviour and phenotype/state ($\text{MLT1}_{\text{Scrounge}}$; $\text{MLT2}_{\text{Scrounge}}$); (3) the effect of immediate stressors on the likelihood/latency to contact the SOC task ($\text{ML2}_{\text{Stress}}$); and (4) individuals’ phenotype/state independent of the interactions between competing activities, scrounging behaviour and stressors ($\text{MLT1}_{\text{Trait}}$; $\text{MLT2}_{\text{Trait,}}$). In case of the model testing the effect of stressors on motivation in the SOC task ($\text{MLT2}_{\text{Stress}}$), I fitted an initial model that included interactions between each of the four stressor variables (i.e. low-risk, high-risk, scratch and groom) and a new fixed effect, the focal-trial interval, to control for differences in the time after the exposure to stress and subsequent testing (median = 13 min, range = 1-49 mins), but excluded phenotypic traits/states and their interactions. If this model resulted in a significant interaction between stressor and interval, an additional model including only the interaction between that significant stressor(s) and phenotype/state was fitted. In all SOC task models, treatment group (P-P, U-P, P-U) and trial number (1-6) were additionally included as covariates to control for differences in cue significance and habituation, respectively, as all tests in this task were conducted on a single day for each participant. Individuals who contacted the task through interrupting another conspecific's trial were excluded from all analyses (n = 7 in the associative learning task; n = 1 in the SOC task). When constructing each model, I included a frailty term (analogous to a random effect in generalised linear mixed effect models) to account for within-individual variation (i.e. repeated measures). Multicollinearity was impossible to test for these of models due to programme restrictions. Nevertheless, models were checked to see that they fit assumptions appropriately. Backwards elimination of non-significant terms was used, until a minimal adequate model was obtained after which, eliminated variables were then added back to the final model to check they remained non-significant. All variables that fell between <0.05 and 0.10 were considered for the minimal adequate model; however only those of significance >0.05 were interpreted.

Degree of exploration of the stimulus

To examine the degree with which individuals examined the task after contacting it, I fitted Generalized Mixed Effects Models using the package "lme4" (Bates et al., 2015). Our initial sample (i.e. all individuals tested) was subsetted to include only those instances where individuals contacted the task. Exploration was considered as the time from when individuals' made contact with the task to when they dropped it and walked away (2 m distance from the task). There was no limit on exploratory time once the task was contacted. Trials which suffered interruptions from conspecifics were not included in this analyses (32 occasions, 28% of all presentations). Following a similar method as the one used in the Cox proportional hazard models above, I fitted, depending on the task, a suite of models that evaluated: (1) the interaction between competing activities and individuals' phenotype/state ($\text{MExT1}_{\text{Activ}}$; $\text{MExT2}_{\text{Activ,}}$ where MLT indicates a Model for Exploratory behaviour of the Tasks 1 and 2 respectively); (2) the interaction between scrounging behaviour and phenotype/state ($\text{MExT1}_{\text{Scrounge}}$; $\text{MExT2}_{\text{Scrounge}}$); (3) the effect of immediate stressors, first testing the interactions between the four stressor variables and the focal-trial interval ($\text{MExT2}_{\text{Stress}}$), and if any were significant, testing in a separate model, only the relationship between that stressor and individuals' phenotype/state; and (4) the effect of the phenotype/state of individuals independent of other variables ($\text{MExT1}_{\text{Trait}}$; $\text{MExT2}_{\text{Trait}}$). In all SOC task models, treatment group (P-P, U-P, P-U) and trial number (1-6) were additionally included as covariates to control for differences in cue significance and habituation respectively. To facilitate convergence, quantitative predictor variables were z-transformed to have a mean of zero and a standard deviation of 1. Individual identity was included as a random intercept in all models and an Observation-Level Random Effect was included as an additional random effect if models showed over-dispersion. In each model, I used variance inflation factors (VIFs) to evaluate multicollinearity, removing variables by stepwise selection from the main model until all remaining variables had VIFs <2.0. Backwards elimination of non-significant terms was used until a minimal model was obtained, after which the eliminated variables were added back into the final model to check they remained non-significant. To reduce the probability of committing Type I Errors, I adjusted the criteria of significance using Bonferroni correction for the two models (i.e. Latency and Exploration) each hypothesis tested (α/n: 0.05/2 = 0.025).

7.4 RESULTS

7.4.1 Extractive Foraging Task

In the extractive foraging task, 111 trials across 37 individuals (mean number of presentations = 3; median = 3; range 1-3) were carried out. In this task, individuals approached and explored either one of the bags on 100 and 79 trials respectively, with a median latency of 2 s (range: 0-111 s) and a median exploratory time of 17 s (range: 0-147 s). Out of the 111 trials, on 32 occasions (29% of all presentations) individuals were engaged in a high-value activity at the time of testing (foraging on all occasions). Through the focal observations, 2455 patch-entry decisions were recorded in 2015, out of which, on 1873 (76%) occasions, individuals had the opportunity to scrounge information from conspecifics (i.e. by entering a foraging patch that was already occupied), while on 582 (23%) occasions, individuals produced information (i.e. foraged from an unoccupied patch).

Likelihood/latency to contact the task

Two of the three models use to explore latency to contact the bags produced a minimum adequate model (Table 7.4). In the first model ($MLt1_{Scrounge}$), there was an effect of an individual's opportunity to scrounge but the effect was dependent upon both age (Fig 7.1A,B) and sex (Fig 7.1C,D). In the first case, as individuals increasingly used social information, they would approach the task more quickly if juvenile but more slowly if adult. In the second case, among those individuals who had the opportunity to use social information, males were faster to approach than females, but slowed to the same speed as females at higher scrounging frequencies. In the second model ($MLt1_{Trait}$), there was a positive effect of age (Fig. 7.2), with juveniles being more likely to contact the task and to do so sooner than adults.

Degree of exploration of the task

In the models tested (Table 7.5), animals spent less time exploring after they had initially been engaged in foraging or grooming (model $MEx1_{Activ}$, Table 7.5; Fig. 7.3A). In addition, juveniles spent more time exploring the bags than adults (Fig. 7.3B). In addition, I found no effect of information use opportunity on exploratory time (model $MEx1_{Scrounge}$, Table 7.5).

Table 7.4 Minimum adequate models obtained from the Cox proportional hazards analyses of factors affecting latency of baboons to approach and contact an extractive foraging task.

	Coefficient	**S.E. of Coefficient**	**Chi-sq**	**Df**	***p***	**CI (+/-)**
$\text{MLT1}_{\text{Scrounge}}$						
Scrounging	-1.39	1.52	0.83	1	0.36	4.92/0.01
Age: Juvenile[1]	-5.46	1.90	8.24	1	**0.004**	0.17/1.02e-04
Sex: Male[2]	5.68	1.97	8.28	1	**0.004**	1.41e+04/6.13
Scrounging*Age	7.89	2.39	10.84	1	**<0.001**	2.93e+05/0.24
Scrounging *Sex	-7.24	2.47	8.55	1	**0.003**	0.09/5.59e-06
Frailty(Individual)			10.84	2	0.25	
Nobs: 110, Nevents: 100, Variance of random effect = 0.03, **l**-Likelihood = -375.7, Likelihood ratio test = 32.89 on 7.15 df, *p* = 3.16e-05						
$\text{MLT1}_{\text{Trait}}$						
Age: Juvenile[1]	0.81	0.28	8.06	1	**0.004**	3.97/1.28
Frailty (Individual)			27.31	14.66	0.02	
Nobs: 110, Nevents: 100, Variance of random effect = 0.34, **l**-Likelihood = -367.4, Likelihood ratio test = 64.34 on 19.02 df, *p* = 7.92e-007						

Shown are: (*i*) name of the models; (*ii*) the covariates assessed; (*iii*) the regression coefficients; (*iv*) the standard errors (S.E.) of the regression coefficient (*v*) Chi-square values; (*vi*) degrees of freedom (Df); (*vii*) *p*-values; and (*viii*) the upper and lower 95% confidence intervals (CI (+/-)) for the hazard ratio. Significant results with values of $p < 0.025$ are highlighted in **bold.** There was no minimum adequate model for competing activities (none of the fixed effects were significant).[1] Reference category: Adult. [2] Reference category: Female.

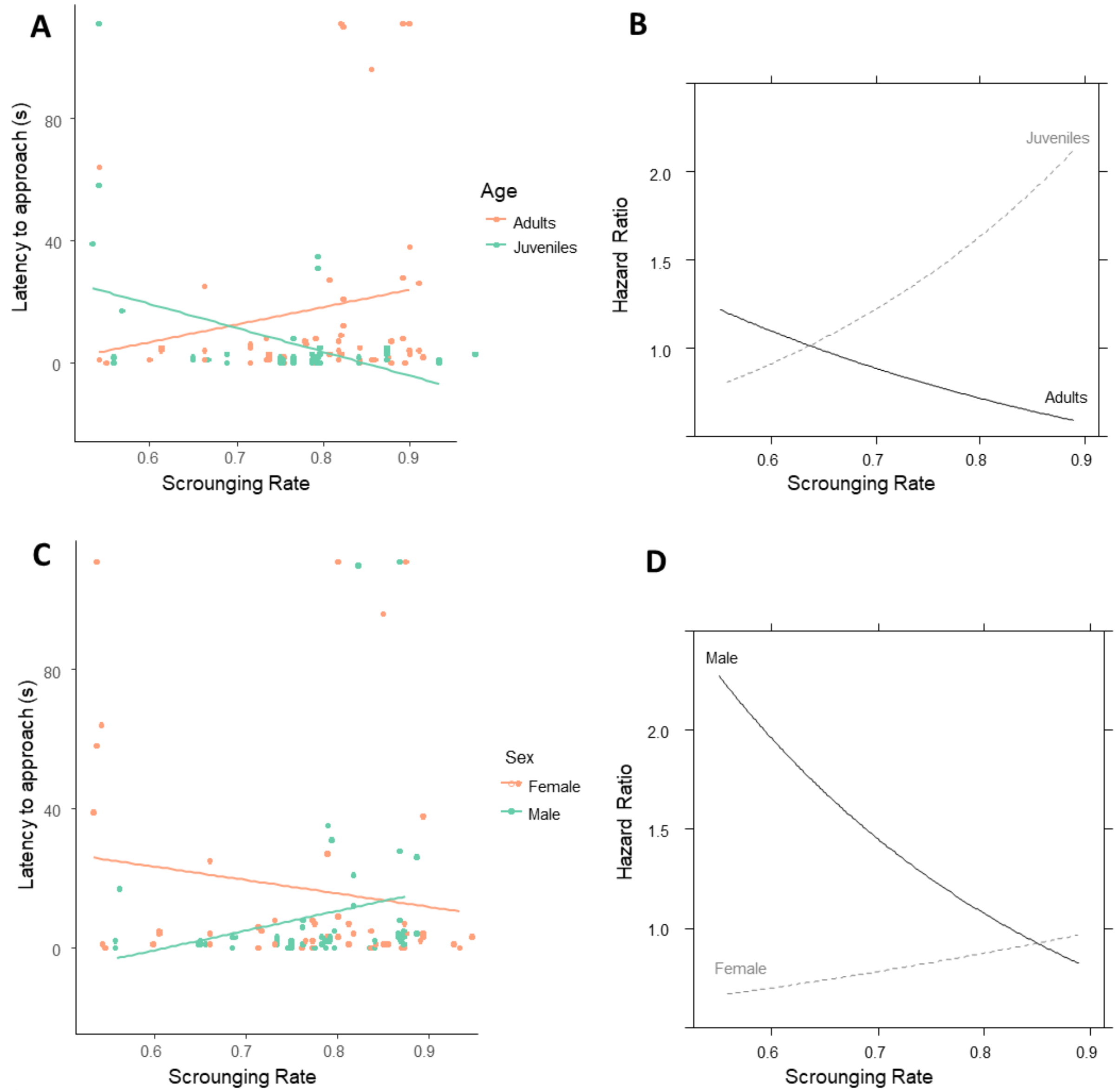

Figure 7.1 The interactions between the likelihood/latency to approach a stimulus and scrounging rate with age class and sex in an extractive foraging task involving two bags of different colour (N = 37). (A) Covariation between the likelihood/latency to first contact with either one of the bags for juveniles (shown in green) and adults (shown in orange) in relation to their scrounging rate (raw data, each point represents an observation point, n = 110); (B) interaction plot showing the hazard ratio of first contact with either bags for juveniles and adults relative to their foraging-based scrounging rate. The cumulative hazard (i.e. hazard ratio) at a scrounging rate t is the ratio of the likelihood of contacting the task at scrounging rate 0 and

scrounging rate t; (C) covariation between the likelihood/latency to first contact with either one of the bags for males (shown in green) and females (shown in orange) in relation to their scrounging rate (raw data, each point represents an observation point, n= = 110); (D) interaction plot showing the hazard ratio of first contact with either bags for males and females relative to their foraging-based scrounging rate. The hazard ratios were calculated from the Cox models (Table 7.3).

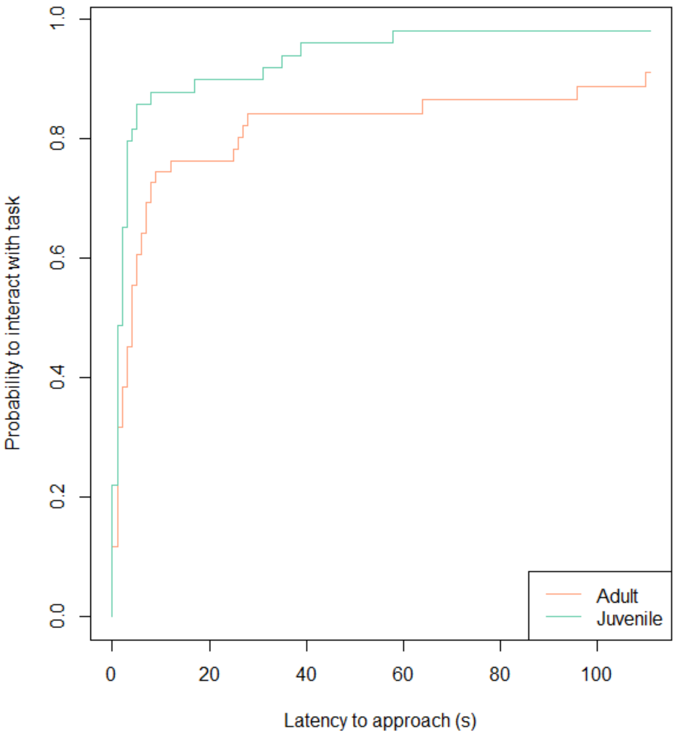

Figure 7.2 Individual differences in the likelihood/latency to approach an extractive foraging task involving two bags of different colour (N = 37). Inverted survival curves of the likelihood/latency of baboons of different ages to contact either one of the bags.

Table 7.5 Minimum adequate models from the GLMM analyses of the exploratory times of wild chacma baboons during an extractive foraging task.

Model	**N_{obs}/ N_{ind}**	**Term**	**Estimate**	**Std. Error**	**t**	***p***
MExT1$_{\text{Activ}}$	93/37	Intercept	2.87	0.14	19.99	
		Activity: Yes[1]	-0.48	0.21	-2.24	**0.02**
MExT1$_{\text{Trait}}$	94/37	Intercept	1.07	0.06	16.4	
		Age: Juvenile[2]	0.32	0.09	3.36	**0.007**

Shown are: (*i*) name of the models; (*ii*) the response variable assessed; (*iii*) the number of observations and individuals for each model; (*iv*) the fixed effects of the minimal models, with their effect sizes and standard errors (estimate, S.E.), test statistic (t) and *p*-values. Significant results with values of $p < 0.025$ are highlighted in bold. [1] Reference category: No. [2] Reference category: Adult.

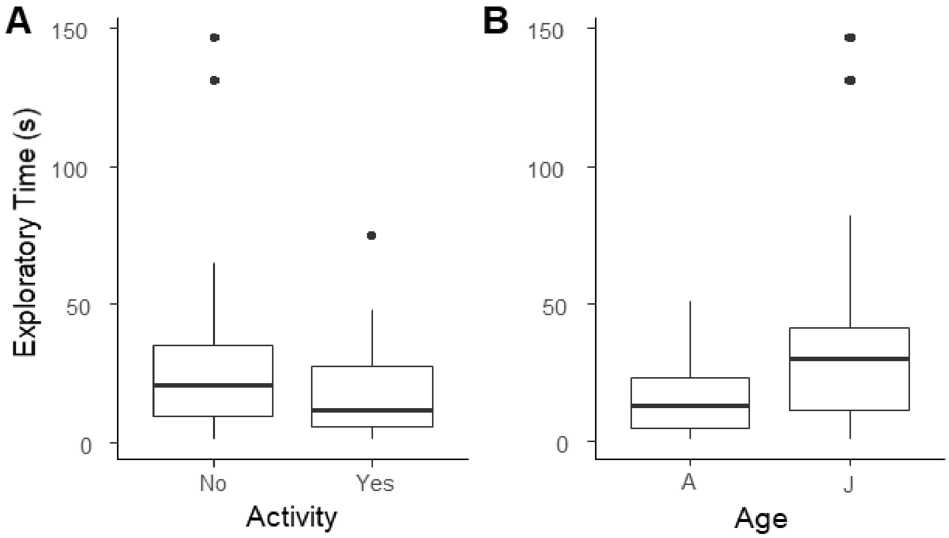

Figure 7.3 Individual differences in the exploration time given to an extractive foraging task involving two coloured bags (N = 37). (A) boxplot of the exploratory time given to either bag and individuals' involvement in a high-value activity (foraging, drinking, grooming) at the start of the trial (Yes, No); (B) boxplot of the exploratory time given to either bag and individuals' age class (A, Adult; J, Juvenile). Total exploratory time was measured as the time individuals spent handling, including sniffing and biting, either one of the bags. The horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

7.4.2 Second-Order Conditioning Task

In the SOC task, 162 trials that included a presentation of the blue square across 27 individuals (mean number of presentations = 6; median = 6; range 1-6) were successfully carried out. Individuals approached and explored the square on 116 out of 162 presentations, with a latency median of 8 s (range: 0-300 s) and a subsequent exploratory time median of 7 s (range: 1-235 s). On 22 occasions (13%), individuals were engaged in other activities when they were presented with the square (15 occasions foraging, 7 occasions grooming). Through the focal observations, 1388 patch-entry events were recorded in 2016, out of which, on 757 (55%) occasions, individuals had the opportunity to scrounge information from conspecifics, while on 631 (45%) occasions, individuals produced information. A median of 3 self-directed behaviours per individual (range 0-25) were recorded per individual prior to each presentation, totalling 606 across all individuals and presentations, out of which 510 events corresponded to self-scratching (79%) and 96 (15%) to self-grooming. On average, I observed 0.74 aggressive events and 2.25 self-directed behaviours prior to each presentation.

Likelihood/latency to contact the task

I found significant effects of competing activity on the latency to contact the blue square (Table 7.6). In this model ($\mathrm{MLT2}_{\mathrm{Activ}}$), individuals who were engaged in a high-value activity at the time of testing had longer latencies to contact the task than those who were not (Fig 7.4). In the second and third models I found no relation between the latency/likelihood to approach and either information preference or any immediate stressors. In the fourth model evaluating the relation between the latency/likelihood to approach and individuals' phenotypic traits/states, lower-ranking individuals had shorter latencies to contact the square and were more likely to do so than higher ranking individuals; however, this result failed to achieve significance once the Bonferroni correction was applied (p = 0.03) and will not be further discussed.

Table 7.6 Minimum adequate models obtained from the Cox proportional hazards analyses of factors affecting latency of baboons to approach and contact a second-conditioning task.

	Coefficient	**S.E. of Coefficient**	**Chi-sq**	**Df**	***p***	**CI (+/-)**
$MLT2_{Activ}$						
Activity: Yes	-0.83	0.21	15.77	1	**<0.001**	0.65/0.28
Social Rank	-1.04	0.47	4.83	1	**0.02**	0.89/0.13
Trial number†	-0.37	0.19	3.86	1	0.04	
Group: PU†	-0.16	0.33	0.24	1	0.63	
Group: UP†	-0.10	0.33	0.09	1	0.77	
Frailty(Individual)			22.53	11	0.02	
Nobs: 158, *Nevents*: 116, Variance of random effects = 0.24, l-Likelihood = -489.9, Likelihood ratio test = 51.94 on 14.28 df, *p* = 3.51e-06						

Shown are: (*i*) name of the models; (*ii*) the covariates assessed; (*iii*) the regression coefficients; (*iv*) the standard errors (S.E.) of the regression coefficient (*v*) Chi-square values; (*vi*) degrees of freedom (Df); (*vii*) *p*-values; and (*viii*) the upper and lower 95% confidence intervals (CI (+/-)) for the hazard ratio. Significant results with values of $p < 0.025$ are highlighted in **bold.** Controlled variables in the model are marked with a cross (†). [1] Reference category: No.

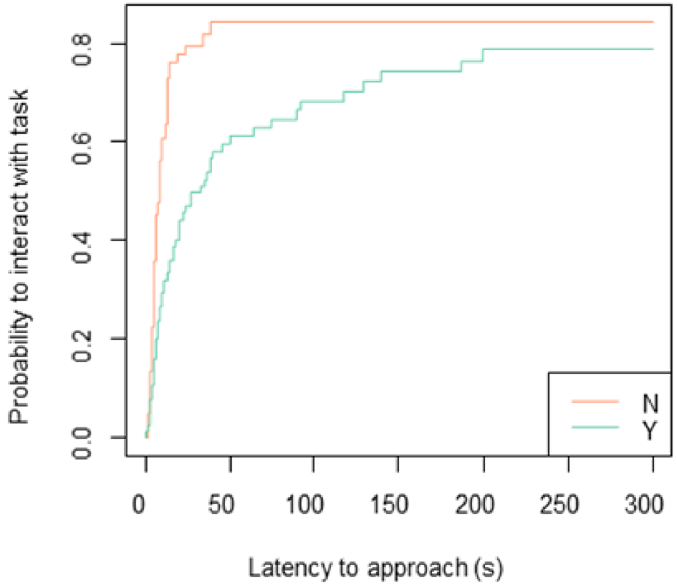

Figure 7.4 Individual differences in the latency to approach a second-order conditioning task involving a blue cardboard square (N = 27). The figure shows inverted survival curves of the likelihood/latency to approach depending on whether or not the baboons were engaged in a high-value competing activity at the time of testing (Y, Yes; N, No).

Degree of exploration of the task

In two out of four models, (all models but scrounging behaviour and the stressor/stress response models), I found significant effects of competing activities and age on the degree of exploration given to the blue square (Table 7.7). In the first model investigating the effects of competing activities, individuals who were engaged in a high-value activity at the time of testing were less likely to explore the task (Fig 7.5A). Similarly, in the second model investigating the main effects of phenotypic traits and states, there was a significant result associated to age, where juveniles had more exploratory time than their adult conspecifics, independently of other traits (Fig 7.5B). I found no relation between the exploratory time of the task and the stressors/stress responses of individuals, based on the high-risk, low-risk and SDB experienced before each presentation of the task. Lastly, in the model evaluating the effect of scrounging behaviour, I found that individuals that had a higher rate of scrounging had then higher exploratory time of the task than producer conspecifics, independent of phenotypic traits; however, this result did not achieve statistical significance after Bonferroni correction (p = 0.03) and will not be discussed further. Lastly, Table 7.8 provides a summary of the results obtained in this task and the extractive foraging task.

Table 7.7 Minimum adequate models from the GLMM analyses of the exploratory times of wild chacma baboons during a second-order conditioning task.

Model	**N_{Obs}/ N_{Ind}**	**Term**	**Estimate**	**Std. Error**	**z**	***p***
$\text{MExT2}_{\text{Activ}}$	115/26	Intercept	4.26	0.59	7.19	
		Activity: Yes^{1}	-0.54	0.21	-2.48	**0.01**
		Trial number†	-0.62	0.19	-3.23	0.001
		Group: PU†	-0.25	0.40	-0.62	0.53
		Group: UP†	-0.50	0.40	-1.25	0.21
$\text{MExT2}_{\text{Trait}}$	116/26	Intercept	3.50	0.32	10.88	
		Age: Juvenile^{2}	1.09	0.32	3.37	**<0.001**
		Trial number†	-0.39	0.04	-9.52	0.005
		Group: PU†	-0.58	0.38	-1.51	0.78
		Group: UP†	-0.78	0.39	-2.00	0.78

Shown are: (*i*) name of the models; (*ii*) the response variable assessed; (*iii*) the number of observations and individuals for each model; (*iv*) the fixed effects of the minimal models, with their effect sizes and standard errors (estimate, S.E.), test statistic (t) and *p*-values. Significant results with values of $p < 0.025$ (excluding the control variables) are highlighted in **bold**. Variables that are controlled for in the models are marked with a cross (†). ^{1} Reference category: No. ^{2} Reference category: Adult.

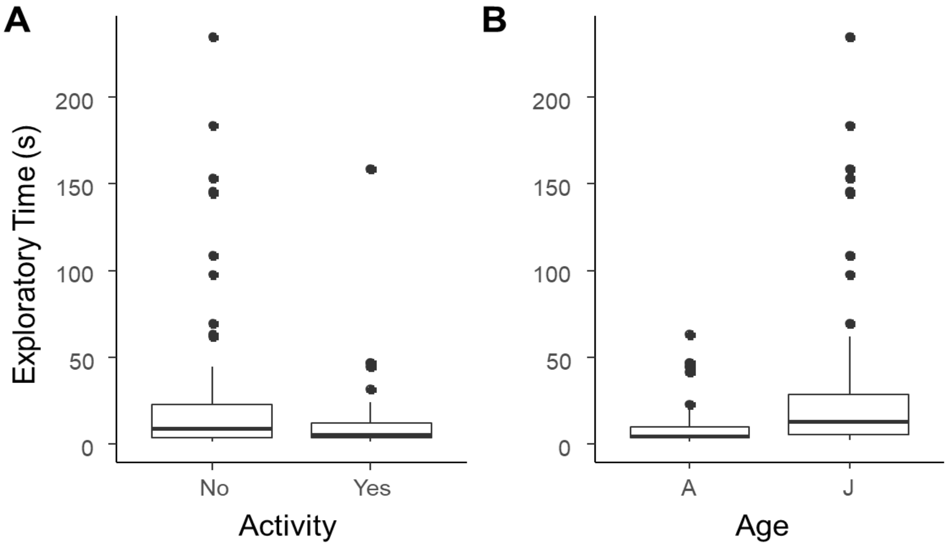

Figure 7.5 Individual differences in the exploration time given to a second-order conditioning task involving a blue cardboard square (N = 27). (**A**) boxplot of the exploratory time given to the blue square according to whether individuals were engaged in a high-value activity at the time of testing (Y, Yes; N, No); (**B**) boxplot of the exploratory time given to the blue square according to individual age. Total exploratory time was measured as the time individuals spent handling, including sniffing and biting, either of the bags. The horizontal line in each box in figure (B) indicate the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

Table 7.8 Summary of the model outputs for the extractive foraging learning and second-order conditioning tasks

Task	Model	Response	Table	Figure	Activity	Scrounge	Stressor	Sex	Age	Rank	Personality
Extractive foraging task	$\text{MLT1}_{\text{Activ}}$	Latency	7.4	–	No	–	–	–	–	–	–
	$\text{MExT1}_{\text{Activ}}$	Exploration	7.5	7.3	Yes	–	–	–	–	–	–
	$\text{MLT1}_{\text{Scroung}}$	Latency	7.4	7.1	–	Yes	–	Yes	Yes	–	–
	$\text{MExT1}_{\text{Scroung}}$	Exploration	7.5	–	–	No	–	–	–	–	– *
	$\text{MLT1}_{\text{Trait}}$	Latency	7.4	7.2	–	–	–	–	Yes	–	–
	$\text{MExT1}_{\text{Trait}}$	Exploration	7.5	7.3	–	–	–	–	Yes	–	–
Second-order conditioning task	$\text{MLT2}_{\text{Activ}}$	Latency	7.6	7.4	Yes	–	–	–	–	–	–
	$\text{MExT2}_{\text{Activ}}$	Exploration	7.7	7.5	Yes	–	–	–	–	–	–
	$\text{MLT2}_{\text{Scroung}}$	Latency	7.6	–	–	No	–	–	–	–	–
	$\text{MExT2}_{\text{Scroung}}$	Exploration	7.7	7.5	–	No	–	–	–	–	–

Task	Model	Response	Table	Figure	Activity	Scrounge	Stressor	Sex	Age	Rank	Personality
	MLT2$_{Stress}$	Latency	7.6	–	–	–	No	–	–	–	–
	MExT2$_{Stress}$	Exploration	7.7	–	–	–	No	–	–	–	–
	MLT2$_{Trait}$	Latency	7.6	7.4	–	–	–	–	–	–	–
	MExT2$_{Trait}$	Exploration	7.7	7.5	–	–	–	–	Yes	–	–

Shown is a summary of the main findings I this study, including: (*i*) the task assessed; (*ii*) the name of each model; (*iii*) the response variable evaluated in each model; (*iv*) the table in which the results of each model can be found; (*v*) the corresponding figure for the results found in each model; and (*vi*) the presence of a significant predictor in each model according to the four hypotheses tested.

7.5 DISCUSSION

In this chapter, I tested four hypotheses about individual variation in the motivation to participate in two cognitive tasks related to: (1) competing activities at the time of testing; (2) information use opportunities of individuals; (3) immediate stressors; and (4) phenotypic traits/states. Throughout the analysis, I found some notable inconsistencies between tasks and between response variables with regards to the latency/likelihood to approach the task and explore it. One possibility in the first case, is that differences between tasks may have been partly because one task offered a reward, while the other did not at first encounter. Thus, for the extractive foraging task, it is likely individuals were more motivated to approach and/or explore the task because the payoff was bigger. Another possibility may be that in the extractive foraging task, each trial was separated by three days, while all measurements in the SOC task were taken on a single day in the life of each animal. As such, it is possible that other untested variables (e.g. daily food intake) determined individuals' motivation to participate on the day they were tested. In the second case, inconsistencies between the response variables may be explained by differences in motivational levels at each stage. Approaching a task and exploring it afterwards, may represent different steps in the engagement process; traits which motivate individuals to approach a task, may not be the same ones that motivate them to spend more or less time exploring it after making contact. Further analysis of these two types of inconsistency is beyond the scope of this study, as there are only two tasks and two response variables from which to draw comparisons. It's worth noting that both years of testing were characterized by a drought period; however, the SOC task was presented at the peak of the drought, when animals' main priority was finding food items rather than engaging with the task. Thus, it's possible that inconsistencies between tasks/responses may have been partly caused by ecological conditions in each year of testing. In the analyses, I found a persistent effect of each of the aspects of interest: competing activities, information use opportunities and immediate stressors, independently and in relation to individuals' phenotypic traits and states, in particular with age. I discuss each of the findings with regards to the four hypotheses I initially proposed to explain variation in the motivation to participate. For the last question, I will discuss the effects of phenotypic traits and states on participation when tested independently from other variables. Interactions will be discussed in the related sections.

H1. Do Competing Activities Influence The Motivation To Participate?

In the extractive foraging task, the availability of a competing activities affected individuals' motivation to participate, albeit only after the task had been contacted. On the other hand, in the second-order conditioning task, individuals' participation was affected by competing activities in both the latency to contact the task and the exploratory time given to it. The results obtained in both tasks suggest that individuals who are engaged in "high-value" activities at the time of testing can be less motivated to participate, as they may either have longer latencies to approach the task and/or explore the task to a lesser degree. These findings are in line with my postdictions and suggest competing activities do indeed influence the motivation to participate in a task. A possible reason for why competing activities were observed to have such a strong effect on individuals' participation on both tasks, may have to do with the effects of two consecutive drought years on individual health/condition and resource abundance at the time of testing, as deviating attention from scarce resources would have been costly. A reason for why studies have so far ignored this effect may be that the large majority of cognitive tasks are carried out in captivity, where the animals are tested in isolation (e.g. Johnson-Ulrich et al., 2018; Vonk & Povinelli, 2011), where there are less opportunities to engage in other activities (Cauchoix et al., 2017) other than the task presented.

H2. Are Individuals Who Have Less Opportunities To Exploit Social Information More Motivated To Participate?

Motivation to participate, was predicted by individuals' use of social information in the extractive foraging task in relation with the phenotypes/states. Specifically, scrounging behaviour determined the latency and likelihood to approach the task in this task. As a generalist and highly social species, chacma baboons rely heavily on social information, as individuals in such species usually benefit from using exploiting information from conspecifics, particularly regarding novel foods (Thornton, 2008). While scrounging permits certain individuals to forage more effectively without the costs of searching for food (Vickery et al., 1991), my results show that the opportunity to use social information may also determine some aspects of behaviour, namely the motivation to approach or engage with novel stimuli. Much of the previous work investigating information use strategies in relation to animal cognition has focused on how information use affects cognitive performance rather than participation. Yet, the results in some of these studies suggest that differences in cognitive performance in relation to information use may also reflect differences in individuals' motivation to engage with a task (e.g. Aplin & Morand-Ferron, 2017; Giraldeau & Lefebvre, 1986). For instance, Aplin & Morand-Ferron (*Parus major*: 2017) who show that scroungers had longer latencies to contact and learn a foraging task in a wild bird population. The lack of studies linking information use differences with motivational traits is surprising, as the level of motivation to participate in a task will invariably determine subsequent performance, as well as bias a sample in favour of those individuals who are more likely to generate information (Katsnelson et al., 2011) because their phenotype or state excludes them from exploiting social information.

The frequency of exploiting information is commonly linked to sociality, as larger groups provide more opportunities for scrounging events, particularly, when food patches can be easily monopolized (Giraldeau & Dubois, 2008; Jones et al., 2017). Yet, according to producer-scrounger theory, a population is never entirely composed of producers or scroungers, but rather, the presence of either is regulated by frequency-dependent selection (Giraldeau & Caraco, 2000; Morand-Ferron et al., 2011). Chacma baboons, often described as opportunists, fall somewhere in the middle, as they have instances of being both producers and scroungers (i.e.Vickery et al., 1991). The present results, along with previous work in this population (e.g. Carter et al., 2013; Lee & Cowlishaw, 2017), indicate that some individuals use one strategy more frequently over the other, and that the use of either is often influenced by their phenotypic traits and/or states. For instance, in the extractive foraging task, I found significant interactions between the scrounging rate and both the sex and age of individuals on the likelihood/latency to approach the task. Following my postdictions, animals who have greater opportunity to scrounge, in this case, males and adults, had longer latencies to the task. However, for females and juveniles, but particularly for the latter, the observed pattern is the opposite of what I postdicted for animals with less opportunities to exploit social information.

In the case of age, juveniles depend on social information to acquire foraging skills (Farine et al., 2015), as this guarantees a reliable way of acquiring experience and, possibly, resources (Galef & Laland, 2005). Compared to juveniles with no preference for social information, scroungers may not only acquire relevant experience to exploit food, but do so without the costs associated with finding foraging patches personally. Consequently, they may be more motivated to engage with novelty. Personally finding food patches may be less costly for adults than for juveniles, as they have the necessary skills to forage efficiently, leading to motivational differences in task participation. In the case of sex, producer females were found to have longer latencies to the task compared to producer males. While females are prone to exploit foraging information from adult males (*Parus major*: Aplin & Morand-Ferron, 2017) or conspecifics, male or female, with whom they are socially close (King et al., 2009). A possible reason why longer latencies were observed in producer females, may be that the cost of producing foraging opportunities is higher for females than for males, as the former may be more vulnerable to displacements from conspecifics, particularly adult males in close proximity. As such, producer females may be less motivated to approach a task, as they may be unwilling to invest time in activities other than foraging. The fact that adults and males were generally less motivated to participate in tasks suggests that they have greater opportunities to exploit information and that it is a highly successful strategy with which to acquire food for them (Morand-Ferron et al., 2011). These patterns are further supported by the fact that males and adults commonly outrank females and juveniles and high-ranking animals are more likely to scrounge off subordinates (Lee & Cowlishaw, 2017). It is possible that different motivational aspects related to scrounging play a role in each of the stages of task participation. Scroungers may be less likely to approach novelty because they have greater opportunity to exploit social cues for resources, but once they do they can afford to spend time exploring.

H3. How Does An Immediate Stressor Affect Individuals' Motivation To Participate?

I found no support for my third hypothesis that immediate stressors would affect individuals' motivation to participate in a task. The lack of results was surprising, not least because stressors determine much of primates' behaviour (e.g. Ostner et al., 2008; Setchell et al., 2010). Depending on whether individuals are exposed to long-term or short-term stressors respectively, primates may see a suppression of sexual traits (e.g. Sapolsky, 2005), impaired cognitive abilities (Lupien et al., 2009) and reduced immune responses (Setchell et al., 2010), or alternatively, maintain individual fitness, by increasing vigilance and respiratory rate, inhibiting non-essential processes and improving cognitive performance (Beehner & Bergman, 2017; Lupien et al., 2009). Based on my postdiction, I would have expected acute-stressors such as the one measured here to affect individuals' motivation, particularly in relation to social rank; yet this was not the case.

A likely explanation for my results, may have to do with insufficient variation in each of the variables used to analyse stress responses. It's likely my analysis lacked the statistical power to discern any effect on task participation. At the same time, it's possible that the variables I chose, were too indirect as a measure of stressors. SDBs, such self-scratching and self-grooming for example, could have been used for hygienic purposes related to parasite load rather than as a stress response (Higham et al., 2009). Likewise, I am unable to discern between nutritional stressors caused by the resource availability at the time of testing and the acute-stressors such as aggressive interactions. In this regard, my study would have benefitted from faecal glucocorticoid measurements at the time of testing or in using the observations of aggression and SDBs collected in the daily focal observations, to potentially compare chronic and acute stress-responses at the time of testing.

H4. How Is Motivation To Participate Influenced By Individuals' Phenotypic Traits/ States?

A consistent pattern throughout the analyses is the effect of age in individuals' motivation to participate as seen in both the likelihood/latency to contact the task and its subsequent exploration. In all cases, my initial postdiction that juveniles would be more motivated to participate in a task were confirmed. When evaluated independently of any interaction in the extractive foraging task, juveniles were more likely to contact the associative learning task at shorter latencies, and later had a higher degree of exploration than adult conspecifics in this task as well as the second-order conditioning task. These results may reflect two aspects of juveniles' behaviour and environments: (1) their highly exploratory nature compared to adults

(Biondi et al., 2010); and (2) their limited access to resources (Johnson & Bock, 2004).

In a social group, poor competitors usually include juvenile animals, (Reader & Laland, 2001). Juveniles lack experience to successfully locate and/or exploit food items (e.g. Desrochers, 1992; Johnson & Bock, 2004; Patterson et al., 2016). The results found here may partly reflect these limitations and may explain individuals' motivation to approach and/or engage with novel objects (Kendal et al., 2005; Reader & Laland, 2001). For instance, experiments with wild meerkats (Thornton & Samson, 2012) and spotted hyenas (Benson-Amram & Holekamp, 2012) reported that juveniles were more exploratory of a cognitive task, perhaps reflecting the tendency of young animals to acquire information in their early-life (Biondi et al., 2010), as well as the motivational shifts observed in adults, who prefer social over non-social stimuli in later life (Almeling et al., 2016). The fact that there were inconsistencies between the latency to approach and the degree of exploration given to the task in the second-order conditioning task may reflect juveniles' motivation to explore and sample their environment (Franks & Thorogood, 2018), even in the absence of food rewards (Benson-Amram & Holekamp, 2012). In both tasks, the effect of age is truly robust, as its presence is consistent throughout the analysis, independently and in relation to the other three variables.

The lack of significant results regarding animals' personality, particularly with regards to latency to approach, seemingly confirms that the variables I analysed here represented motivational differences, rather than neophobic responses. Nevertheless, I do not rule out that some baboons failed to participate approach and/or explore either task due to reasons other than motivation. For instance, it is equally possible that the latency observed here is neither in response to motivation or novelty, but rather reflects a behaviour some individuals adopt in order to avoid the spread of information. Animals may purposely delay approaching the task to avoid attracting the attention of conspecifics (Beauchamp, 2006) and either lose the reward, or risk being recipients of aggression. Unfortunately, these variables, along with stress responses, are difficult to differentiate from one another, a common problem found in other studies evaluating participation (e.g. van Horik et al., 2016). Moreover, it is difficult to estimate the effect the presence of a human experimenter has on animals' participation in a task. Numerous studies detail the influence human experimenters have on cognitive performance (e.g. Call et al., 1998; Damerius et al., 2017), including contact with tasks (Kenward et al., 2006). It's likely wild animals have a more fearful response to human observers than their captive conspecifics (e.g. Cowlishaw, 2010), which may determine individuals' level of participation in novel tasks. Given that this study was based on postdictions, independent replication must be conducted to consider these alternative explanations or provide robustness. How motivation changes year to year, depending on the prevailing ecological conditions and changes in the individuals' phenotype, should be an area of interest for researchers studying cognition in the wild. The generalisability of results will depend on the number of animals that fully participate, as conclusions from small samples may simply not provide enough information about the species.

Chapter 8

Using Cognitive Tasks To Evaluate Variation In Foraging Techniques In Wild Chacma Baboons

8.1 ABSTRACT

To successfully acquire resources, animals may develop a number of techniques with which to forage. The development of these techniques will largely depend on the resources available, as well as the physical and social characteristics of a given species. Previous research has focused on the differences in foraging techniques between groups of the same or different species; yet, so far, research on state-dependent variation in foraging techniques and its associated causes has been scarce, and no experimental studies exist. Cognitive tasks may provide a way in which to quantify foraging techniques as they commonly provide animals with food rewards. Here, I investigated a suite of hypotheses related to foraging techniques, namely, the manipulation of food items and physical posture adopted whilst eating, in two groups of wild chacma baboons during two cognitive tasks involving corn kernels. These two aspects served as the basis to test five hypotheses: (1) that vulnerable individuals are more likely to be interrupted by conspecifics in a task; (2) that vulnerable individuals are more likely to use a given technique; (3) that different techniques reduce the foraging information available to conspecifics to avoid interruptions; (4) that different techniques allows vulnerable individuals to eat the

rewards more effectively (i.e. more quickly); and (5) that aggressive interruptions are more likely to predict the use of a technique. I found support for all my hypotheses, although this was variable according to the age and social rank of individuals as well as the task tested. My results suggest the use of a given technique may be phenotype/state-dependent and that vulnerable individuals, may use techniques with which to forage to avoid aggressive interruptions from conspecifics and access high-quality food rewards.

8.2 INTRODUCTION

The literature behind foraging behaviour argues that animals should forage optimally, in ways that maximize their fitness (Pyke, 1984), for example by choosing the food items that offer the greatest nutritional reward for the lowest foraging effort. Much research has focused on the food choices animals make during foraging (Marshall et al., 2012), as well as the trade-offs involved between foraging and other activities (Cowlishaw, 1997; Dunbar, 1992); yet very little research has been conducted on how animals develop and use specific foraging techniques to access and consume their food. The use of the term “technique”, here refers to the handling/processing methods involved in food harvesting and consumption once the food has been located. Whether a given foraging technique is developed in the first place will likely depend on the resources that are available in the animals’ immediate environment, as well as the efficiency of such behaviour and the value of the reward obtained (Boesch & Boesch, 1990). While much has been recorded on the existence of differences in foraging techniques between populations of a given species (e.g.

great tits, *Parus major*: Aplin et al., 2015; bottlenose dolphins, *Tursiops* sp.: Krützen et al., 2005), in particular primate species (e.g. chimpanzees, *Pan troglodytes:* Biro et al., 2003; Japanese macaques, *Macaca fuscata*: Kawai, 1965; red-fronted lemurs, *Eulemur rufifrons*: Schnoell & Fichtel, 2012; vervets, *Cercopithecus aethiops*: van de Waal et al., 2013), there is little information regarding inter- and intra-individual differences in foraging techniques within populations, including its possible causes (but for an exception, see van Schaik et al., 2003).

In every species, individuals differ to some degree in their foraging behaviour, due to physical, ecological or social constraints (van Schaik et al., 2003). For example, juveniles and adults commonly show different foraging techniques because juveniles either lack sufficient experience to exploit resources in the same ways as adults (Gochfeld & Burger, 1984), have morphological differences from adults (Marchetti & Trevor, 1989), or experience learning constraints (Franks & Thorogood, 2018). In brown pelicans (*Pelecanus occidentalis*), for instance, foraging requires individuals to plunge dive into the ocean, a technique that takes up to three years to develop to have high rates of success (Carl, 1987). Likewise, van Schaik et al. (2003) reported differences in tool use within an orangutan (*Pongo pygmaeus*) population due to variation in opportunities to observe techniques from their kin during a juvenile period. This potential lack of experience, capability, and learning opportunities in juvenile foragers may put them at a disadvantage compared to experienced, able, and competent adults. Similarly, individuals' access to food can, in some species, be determined by their social status (Whitten, 1983). Lower ranking animals may adopt different foraging techniques from higher ranking animals because it is common for subordinates, to have limited access to resources and to forage on lower quality items, particularly when conditions are unfavourable (e.g. Murray et al., 2006). In contrast, dominant animals often use aggression to exclude subordinates from monopolisable resources (Lee & Cowlishaw, 2017) and commonly exploit information about foraging opportunities from such conspecifics through scrounging behaviour (Giraldeau & Caraco, 2000). Group-living involves directly competing with conspecifics, maintaining fitness whilst avoiding costly physical confrontation over desired resources. When encountering valuable food items, individuals may turn to techniques that allow them to consume highly preferred resources, whilst avoiding interference from conspecifics or kleptoparasitism (e.g. *Cebus apella*: di Bitetti & Janson, 2001). Thus, in order to compete with older, more experienced and/or dominants, vulnerable animals, such as subordinates or juveniles, could turn to surreptitious behaviours to limit the amount of information towards conspecifics or similarly, that involves faster consumption of the food.

Cognitive tasks may present a valuable opportunity to explore individual differences in foraging techniques, as they commonly involve food rewards. Studies in captivity rely on isolating animals during testing (e.g Johnson-Ulrich et al., 2018), effectively eliminating any social pressure that may limit individuals' feeding. For instance, Cronin et al. (2014) reported chimpanzees (*Pan trogolodytes*) obtained fewer rewards when tested alongside conspecifics, particularly high-ranking ones, compared to when they were tested alone. Moreover, captive animals are allowed a considerable amount of time in which to access and consume the food reward involved in a task (e.g. Schmitt et al., 2012); therefore, there may be less pressure for animals to use techniques that allow them to eat food more quickly. Cognitive tasks in the wild can thus provide us with valuable information about how and when are animals likely to use a given foraging techniques the benefits such behaviours can provide. In this study, I aimed to evaluate individual differences in foraging behaviour in two groups of wild chacma baboons while they solved two associative learning tasks involving a food reward. One of the prominent characteristic of this species is its strict linear dominance hierarchy, where ranks are inherited, in the case of philopatric females, and determined competitively, in the case of adult males (Cheney & Seyfarth, 2007). In addition, there is a significant juvenile period. Females reach adulthood around 4 years of age, developing a sexual swelling that signals fertility (Huchard et al., 2009); while males become adult at around 9 years of age, after which they disperse from their natal troop (Cheney & Seyfarth, 2007). The high competitiveness of this species may drive individuals, particularly vulnerable ones like juveniles and low-ranking individuals, to forage in ways that maximise their fitness, for example by avoiding interruptions from conspecifics or consuming food items rapidly.

I aimed to test five hypotheses about individual differences in foraging techniques, the characteristics of those techniques, and the circumstances under which they are adopted: (H1) that vulnerable individuals are more likely to be interrupted during each task; (H2) that vulnerable individuals are more likely to use an inconspicuous foraging technique that limits the spread of information; (H3) that using an inconspicuous technique allows vulnerable individuals to avoid interruptions in the current trial; (H4) that some foraging techniques allow faster consumption of food resources than others; and (H5) that after being supplanted and losing the food reward to a conspecific, individuals are more likely to use an inconspicuous technique in the following trial. To test these hypotheses, I defined whether or not a foraging technique was ‘inconspicuous’ according to two axes, one ‘mechanical’, based on how conspicuously individuals manipulated their food during consumption; the other ‘physical’, based on how conspicuously individuals positioned themselves while eating the food items. This study was conceived from the behavioural observations made while testing individuals with each cognitive task. As such, the hypotheses presented here are based on postdictions.

8.3 MATERIALS & METHODS

8.3.1 Study Site And Species

This study was carried out over two field seasons of 6 and 5 month duration over two years (April-September 2015; May-September 2016) on two fully-habituated troops (J and L Troops) of chacma baboons at the Tsaobis Baboon Project in Tsaobis Nature Park (15° 45’E, 22° 23’S) on the edge of the Namib Desert, Namibia. Refer to Chapter 3 for details on this species, population, and study site.

8.3.2 Experimental Protocol

I had previously tested a group of wild chacma baboons with two associative learning tasks (referred to here as associative learning tasks 1 & 2), that involved a food reward. The first task involved two piles of coloured kernels differing in palatability, which tested the ability of individuals to associate a visual stimulus with a specific taste. The second task was a second-order conditioning task which evaluated the ability of individuals to make sequential associations. These tasks allowed me to assess and quantify the differences in the behavioural patterns used to eat food-items throughout each trial as they visibly offered food items.

Associative learning task 1

A representative sample of 38 baboons was tested over the months of July-September 2015. I presented individuals with a novel associative learning task involving two coloured piles of approx. 20 corn kernels (coloured red and green) which differed in taste: one was soaked in a non-toxic bitter solution (i.e. unpalatable) and the other was not (i.e. palatable). In this task, individuals were assessed over five trials (mean number of presentations = 4.3, median = 5, range 3-5) with a three-day interval between each presentation (mean; median re-test interval: 3.7; 3.00 days). See Chapter 4 for a full description of this task.

Associative learning task 2

A representative sample of 27 baboons) was tested over the months of June-September 2016. I conducted a second-order conditioning task, which consisted in conditioning individuals over series of presentations involving pairing a pile of approx. 20 corn kernels (naturally coloured) with a clicker and a blue cardboard square with a clicker. Each individual was tested on 9 separate occasions separated into three phases over the course of a single day. Each phase involved three presentations with an average inter-trial interval of 57 min (range 20-227 min), such that a full assessment lasted approx. 9 hours in total. See Chapter 6 for a full description of this task.

8.3.3 General Protocol

Observers followed both groups of baboons on foot from dawn to dusk. All individuals over four years of age were individually identifiable. Observers moved throughout the troop, using the freely available software Cybertracker (www.cybertracker.org) on individual smart phones (Samsung Galaxy S4, Samsung, Seoul, South Korea) to record dominance and social interactions *ad libitum*. Refer to Chapter 3 for details on the general protocol followed.

Individual differences

For details on how age and social rank were measured please refer to Chapter 3. Age was established in 2015 and re-assessed the following year to account for changes to adulthood in males and females. Dominance hierarchies were calculated for each year of study.

Cognitive tasks

To test the five hypotheses proposed, I used the videos taken for each trial in each task to obtain two behavioural patterns that individuals used to eat the corn kernels: (1) mechanical manipulation of food items and (2) the physical posture adopted whilst eating the food items. It is important to note that while individuals could adopt a mechanical manipulation whilst in a given physical posture (see Fig. 8.1), these variables were classified separately to facilitate analyses and interpretation.

Mechanical manipulation of food items was thus classified as either, individuals picking up food items with both hands before transferring them to their mouth or individuals picking up food items directly with their mouth (referred to as mouth-to-substrate technique); while the physical posture was classified as either individuals sitting down or individuals crouching whilst feeding. I classified individuals' posture as sitting down when their ischial callosities (i.e. coarse patches located in the pelvic bones on which they sit) touched the substrate and crouched when their ischial callosities were at a ≥30° angle relative to the substrate. Individuals positioned at an angle <30°, were considered as sitting down. Crouching behaviour was only observed in a foraging context in this population; however, studies on other baboon species have likewise described individuals adopting the two physical postures evaluated here whilst foraging. Juvenile yellow baboons (*Papio cynocephalus*) for instance, are more likely to pull food items with their molars lifting their callosities for leverage, while adults usually sit and use their hands whilst foraging (Rhine & Westlund, 1978). Figure 8.1A, B and C shows exemplars of individuals' techniques during assessments with loose corn kernels. Using a mouth-to substrate manipulation and/or adopting a crouching posture were determined to be inconspicuous behaviours. The rapid alternate movement of hands to and from the mouth chacma baboons use whilst feeding is often a signal to conspecifics that food is being consumed. Likewise, it's possible that sitting down whilst foraging increases the visibility of an individual towards conspecifics. Thus, picking items directly with the mouth or crouching over the food as determined here, may have the advantage of limiting the visibility of the arm movement or body compared to when animals are using both hands to pick food or sitting down. Likewise, adopting such inconspicuous behaviours may limit the distance from the floor to the mouth of individuals, allowing animals to eat the food items more quickly.

For each task, I additionally recorded any aggressive interaction that resulted in an interruption in each trial. Lastly, I recorded in each task the amount of time spent eating both piles of corn kernels (s). Each task had differences in the number of mechanical manipulations and physical postures adopted. In the associative learning task 1, both mechanical manipulations (i.e. hands, mouth-to-substrate) and physical postures (i.e. sit, crouch) were observed; while in the associative learning task 2 only differences in physical postures were observed, as all individuals ate the food items using both hands (i.e. no mouth-to-substrate) in all trials. Consequently, the analysis for the associative learning task 1 included both, manipulation and posture techniques; while the analysis of associative learning task 2 included only the latter techniques. Table 8.1 summarises the occurrence of each technique, mechanical or physical.

Table 8.1 Summary of the occurrence of each technique in each task

		Task 1	**Task 2**
Mechanical manipulation	Hands	96	81
	Mouth	32	0
Physical posture	Sit	50	48
	Crouch	78	33

Shown are the number of observations of each technique, mechanical manipulations or physical postures, observed in the associative learning task 1 and 2.

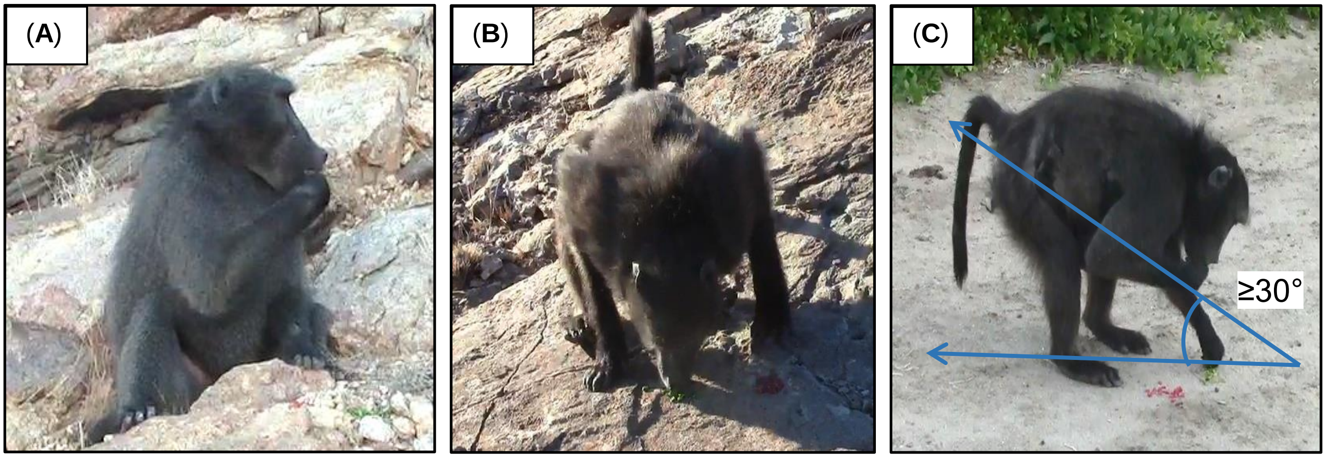

Figure 8.1 Individuals' mechanical manipulations and physical postures in the two cognitive tasks; (**A**) an adult baboon sitting down whilst eating the corn kernels with both hands; (**B**) a juvenile baboon crouches to eat the corn kernels directly with its mouth (mouth-to-substrate); and (**C**) an adult baboon crouches >30° in relation to the substrate whilst eating the corn kernels using both hands.

8.3.4 <u>Statistical Analysis</u>

All analyses were fitted in the R environment (version 3.2.3, 2015). To test my five hypotheses in each of the two cognitive tasks, I fitted a series of Generalized Linear Mixed effects Models (GLMMs: package "lme4": Bates et al., 2015) (although see analysis description for the H2), using four possible response variables: (1) the occurrence of aggression in a given trial; (2) the mechanical manipulation used to eat the corn kernels; (3) the physical posture individuals had while eating the corn; or (4) the time spent eating the food items provided in every task (s). How these response variables were coded depended on the model and task in question and are fully described in each section below. Although not all hypotheses specify it, I include the effects of age class and social rank of individuals in all models to explore the possibility that the proposed effects were more pronounced among vulnerable individuals. Unless explicitly mentioned, models were initially built using the full sample in each task. See Table 8.2 for the outline of the models used to evaluate foraging techniques in each task.

H1: Vulnerable individuals are more likely to be interrupted

To test my first hypothesis, that vulnerable individuals are more likely to be interrupted during a task, I fitted for each one of the tasks, a model that included the occurrence of aggression during each trial as the response variable (0, No; 1, Yes) and the social rank and age class of individuals as fixed effects (Model Task $1_{Vul;}$ $MT2_{Vul}$).

H2: Vulnerable individuals are more likely to use an inconspicuous technique

To test my second hypothesis, that vulnerable individuals are more likely to use inconspicuous techniques in each task, I first fitted two Cumulative Link Mixed Models ("ordinal" package: Christensen, 2011) in the associative learning task 1 ($MT1_{MTech;}$ $MT1_{PTech}$). I used cumulative models because in the associative learning task 1 individuals were provided with two piles of kernels for which they could use one or both manipulation/posture techniques to eat either or both piles of kernels. Thus, the levels of the response variables in this task were ordered from least inconspicuous to most inconspicuous for mechanical manipulations (0, individuals ate both piles of kernels using their hands; 1, individuals ate one pile of kernels using their hands, the other with their mouth directly; 2, individuals ate both piles of kernels using their mouth directly) and physical posture (0, individuals were sitting down whilst eating both piles of kernels; 1, individuals were sitting whilst eating one pile of kernels and crouched while eating the other; 2, individuals were crouched whilst eating both pile of kernels). The age class and social rank of individuals were included as main effects in each model. In the associative learning task 2, I fitted a single GLMM with a binomial error link structure that included as a response variable the physical posture (0, Sit; 1, Crouch) individuals adopted whilst eating from the single pile of corn provided ($MT2_{Tech}$). Similar to the model for the associative learning task 1, age class and social rank were included as main effects.

H3: Inconspicuous techniques allow vulnerable individuals to reduce aggressive interruptions

To test my third hypothesis, that inconspicuous techniques allow vulnerable individuals to reduce interruptions, I used the occurrence of aggression in each trial as the response variable (0, No; 1, Yes). Two GLMM models with a binomial error link were fitted in the associative learning task 1, each evaluating the effects of mechanical manipulations ($MT1_{MInt}$) and physical posture ($MT1_{PInt}$) respectively. Due to a lack of sufficient data in the associative learning task 1, mechanical manipulations used to eat both piles of kernels was coded as follows: 0, individuals ate both piles of kernels using both hands; 1, individuals ate one or both piles of kernels using their mouth directly. Likewise, the physical posture whilst eating each pile of kernel was classified as: 0, individuals ate both piles whilst sitting down; 1, individuals ate one or both piles of kernels in a crouching position. Both models additionally included an interaction between the respective technique and individual age and social rank. For the associative learning task 2, I fitted a GLMM that included the physical posture of individuals (0, Sit; 1, Bent) in an interaction with both, age class and social rank ($MT2_{Int}$).

H4: Some foraging techniques allow individuals to eat food items more quickly

To test my fourth hypothesis, that some foraging techniques allow individuals to eat more quickly, I used the time spent eating the corn kernels (s) as the response variable. Because this response variable required that all individuals eat the same number of kernels, I focused on analysing only uninterrupted trials in each task. For each task, I fitted a model that included the main effects of mechanical manipulations (for the associative learning task 1) and physical posture (for the associative learning task 1 and 2), age class and rank, and their respective interactions ($MT1_{Un}$; $MT2_{Un}$). Mechanical behaviours and physical position in the associative learning task 1 and 2 were classified as stated in the analysis for H3.

H5: Previous aggression predicts the use of an inconspicuous technique

To test my fifth prediction that animals who had previously received aggression during a trial would be more likely to use an inconspicuous technique, I fitted, for the associative learning task 1, two models with a logit link function to account for binomial error structure ($MT1_{MPrev}$; $MT1_{PPrev}$) using as the response variable either the mechanical manipulation or physical posture used to consume both piles of kernels presented. For mechanical manipulations, the response variable was coded as follows: 0, individuals consume both piles of kernels using both of their hands; 1, individuals consume at least one pile of kernels directly with their mouth. For physical posture, the response variable was coded as follows: 0, individuals consume both piles of kernels whilst sitting down; 1, individuals consume at least one pile of kernels whilst crouching over the food items. Each model included an interaction between trial interruptions in the previous trial (0, No; 1, Yes) and age class and rank respectively. A similar model was fitted for the associative learning tasks 2 ($MT2_{Prev}$), which employed as the response variable the physical posture (0, Sit; 1, Crouch) used whilst consuming the single pile of kernels and included the interaction between previous aggressive interruptions and age class and social rank.

All models for all five hypotheses included individual identity as a random effect. There were no co-variances where the Spearman correlation $|r|$ was >0.70 between any of the fixed effects (Appendix S5, Table S5.1). To facilitate convergence, quantitative predictor variables were z-transformed to have a mean of zero and a standard deviation of 1. Additionally, I used variance inflated factors (VIFs) to evaluate for multicollinearity and did a stepwise selection from the main model until all remaining variables had VIFs <2.0 Backwards elimination of non-significant terms was used, until a minimal model was obtained after which eliminated variables were then added back to the final model to check they remained non-significant.

Table 8.2 Model outline for each of the hypotheses tested.

Task	Model	Hypothesis	Sample	Response	Fixed effects
Associative learning task 1	$MT1_{Vul}$	H1	Full sample	Trial Interruptions	Age Social rank
	$MT1_{MTech}$	H2	Full sample	Mechanical Manipulations	Age Social rank
	$MT1_{PTech}$	H2	Full sample	Physical Posture	Age Social rank
	$MT1_{Int}$	H3	Full sample	Trial Interruptions	Mechanical. B* Physical. P* Age Social rank
	$MT1_{Un}$	H4	Uninterrupted trials	Time spent eating	Mechanical. B* Physical. P* Age Social Rank
	$MT1_{MPrev}$	H5	Full sample	Mechanical Manipulations	Previous interruption* Age Social Rank
	$MT1_{PPrev}$	H5	Full sample	Physical Posture	Previous interruption* Age Social Rank
Associative learning task 2	$MT2_{Vul}$	H1	Full sample	Trial Interruptions	Age Social rank
	$MT2_{Tech}$	H2	Full sample	Physical Posture	Age Social rank
	$MT2_{Int}$	H3	Full sample	Trial Interruptions	Physical. P* Age Social rank
	$MT2_{Un}$	H4	Uninterrupted trials	Time spent eating	Physical. P* Age Social Rank
	$MT2_{Prev}$	H5	Full sample	Physical Posture	Previous interruption* Age Social Rank

Shown are: (*i*) the name of the task; (*ii*) the name of the model; (*iii*) the hypothesis that model is testing; (*iv*) the sample used; (*v*) the response variable used; and (*vi*) the fixed effects used. Variables marked with (*) indicate interactions between that fixed effect and the age and social rank of individuals.

8.4 RESULTS

8.4.1 Associative Learning Task 1

The baboons usually hand-picked the first pile of corn kernels on 124 occasions (76%) and continued to do so for the second pile on 121 occasions (74%). The baboons used a mouth-to-substrate manipulation on 35 occasions (21% of trials) to eat the first pile of corn and continues to do so for the second pile in only 11 occasions (7%). In 23 (14%) trials, individuals switched their foraging technique between piles; of these 23 trials, on 21 occasions (91%) they switched from the mouth-to-floor technique to eating the corn kernels with both hands. Individuals switched their technique whilst still eating corn from the first pile of kernels on 27 occasions (17% of trials). Baboons sat whilst eating the first pile of kernels on 56 occasions (34.5) and continued on this posture for the second pile on 64 occasions (40%). Meanwhile, on 100 occasions (62%), the baboons crouched over whilst eating the first pile and continued to do so for the second pile on 65 (40%). Baboons changed from crouching to sitting down on 12 cases (7.4% of trials). Baboons ate the corn kernels from both piles in a median average of 15s (range: 0-267 s), being interrupted on 73 occasions (45% of trials) before they could finish both piles of corn.

In line with my first hypothesis (H1), I found that juveniles and low-ranking animals were more likely to be interrupted (Table 8.3, $MT1_{Vul}$, Figs 8.2A, B respectively). Similarly, in line with my second hypothesis (H2), I found that low-ranking animals were more likely to adopt an inconspicuous physical posture (Table 8.4, $MT1_{PTech}$, Fig 8.3). I also found evidence that juveniles were more likely to use an inconspicuous mechanical manipulation, although this result did not quite achieve statistical significance (Table 8.4, $MT1_{MTech}$, p=0.055). In support of my third hypothesis (H3), low-ranking animals had a lower probability of being interrupted when they used an inconspicuous mechanical manipulation (Table 8.3, $MT1_{Int}$, Fig 8.4). I also found juveniles were less likely to be interrupted when they adopted an inconspicuous physical posture, but this interaction did not quite achieve statistical significance (Table 8.3, $MT1_{Int}$, p=0.05). In support of my fourth hypothesis (H4), I found that crouching animals eat more quickly than those sitting down (Table 8.3, $MT1_{Un}$, Figs 8.5A); I also found that individuals adopting a more inconspicuous mechanical behaviour eat faster, but this result did not quite achieve statistical significance (Table 8.3, $MT1_{Un}$, p=0.05). Additionally, juveniles generally eat faster than adults, although this was independent of the techniques investigated (Table 8.3, $MT1_{Un}$, Fig 8.5B). Lastly, in line with my fifth hypothesis (H5), I found that individuals who were recipients of aggression in a previous trial were more likely to use an inconspicuous mechanical behaviour to eat at least one pile of kernels (Table 8.3, $MT1_{MPrev}$, Fig 8.6A). A similar effect was also observed on the recipients' use of more inconspicuous physical positions, but this was only evident in high-ranking animals (Table 8.3, $MT1_{PPrev}$, Fig 8.6B). Table 8.5 provides a summary of these results.

Table 8.3 GLMM analyses of the foraging techniques of wild chacma baboons in an associative learning task using coloured corn kernels and second-order conditioning (SOC) task.

Model	**N_{obs} / N_{ind}**	**Deviance**	**Term**	**Estimate**	**S.E.**	***z***	***P***
MT1$_{\mathbf{Vul}}$	161/ 38	209.1	Intercept	-0.60	0.23	-2.60	
			Age: Juveniles[1]	-0.33	0.32	2.87	**0.004**
			Social Rank	0.94	0.16	-1.98	**0.04**
MT1$_{\mathbf{Int}}$	125/ 37	127.3	Intercept	-3.72	1.09	-3.41	
			Mech. Manipulation[2]	-1.12	0.57	-1.96	**0.04**
			Physical Posture[3]	4.16	1.20	1.25	**<0.001**
			Social Rank	0.44	0.35	3.43	0.20
			Age: Juveniles[1]	3.13	1.14	2.74	**0.006**
			Mechanical* Rank	-1.63	0.70	-2.33	**0.01**
			Physical*Age	-2.41	1.25	-1.92	0.05
MT1$_{\mathbf{Un}}$	68/ 32	580.1	Intercept	3.73	0.11	31.44	
			Mech. Manipulation[2]	0.45	0.23	1.95	0.05
			Physical Posture[3]	-0.84	0.19	-4.38	**<0.001**
			Age: Juveniles[1]	-0.54	0.18	-3.02	**0.002**
MT1$_{\mathbf{MPrev}}$	97/ 36	101.0	Intercept	-2.62	0.75	-3.48	
			Aggression in previous trial: Yes[4]	1.51	0.63	2.39	**0.01**
			Age: Juveniles[1]	1.26	0.72	1.73	0.08
MT1$_{\mathbf{PPrev}}$	97/ 36	93.7	Intercept	0.79	0.39	1.99	
			Aggression in previous trial: Yes[4]	0.64	0.56	1.15	0.25
			Social Rank	-1.76	0.50	-3.51	**<0.001**
			Aggression*Rank	1.54	0.68	2.26	**0.02**
MT2$_{\mathbf{Tech}}$	81/ 27	68.8	Intercept	-0.73	0.75	-0.96	
			Social Rank	-3.10	1.19	-2.58	**0.009**
MT2$_{\mathbf{Un}}$	56/ 25	333.6	Intercept	2.56	0.15	16.25	
			Physical Position[5]	-0.29	0.11	-2.64	**0.008**
			Social Rank	0.33	0.20	1.68	0.09
MT2$_{\mathbf{Prev}}$	81/ 27	68.8	Intercept	-0.73	0.75	-0.96	
			Social Rank	-3.10	1.19	-2.58	**0.009**

Shown are: (*i*) name of the models; (*ii*) the response variable assessed; (*iii*) the number of observations and individuals for each model; (*iv*) the fixed effects of the minimal models, with their effect sizes and standard errors (estimate, S.E.), test statistic (z) and *p*-values. Significant results with values of $p < 0.05$ are highlighted in **bold.** [1] Reference category: Adult. [2] Reference category: use mouth to eat one or both piles of kernels. [3] Reference category: crouch over one or both piles of kernels. [4] Reference category: No. [5] Reference category: Crouched

Table 8.4 Cumulative Link Mixed Models analyses of the foraging techniques of chacma baboons in an associative learning task involving coloured corn.

Model	**Response**	**N_{obs} / N_{ind}**	**Term**	**Estimate**	**S.E.**	***z***	***p***
$\mathrm{MT1}_{\mathrm{PTech}}$	Physical Position	127/ 37	Social Rank	-1.20	0.28	-4.19	**<0.001**

Results shown here represent models with an ordered response variable. Shown are: (*i*) name of the models; (*ii*) the number of observations and individuals for each model; (*iii*) the fixed effects of the minimal models, with their effect sizes and standard errors (estimate, S.E.), test statistic (t) and *p*-values. Significant results with values of $p < 0.05$ are highlighted in **bold**.

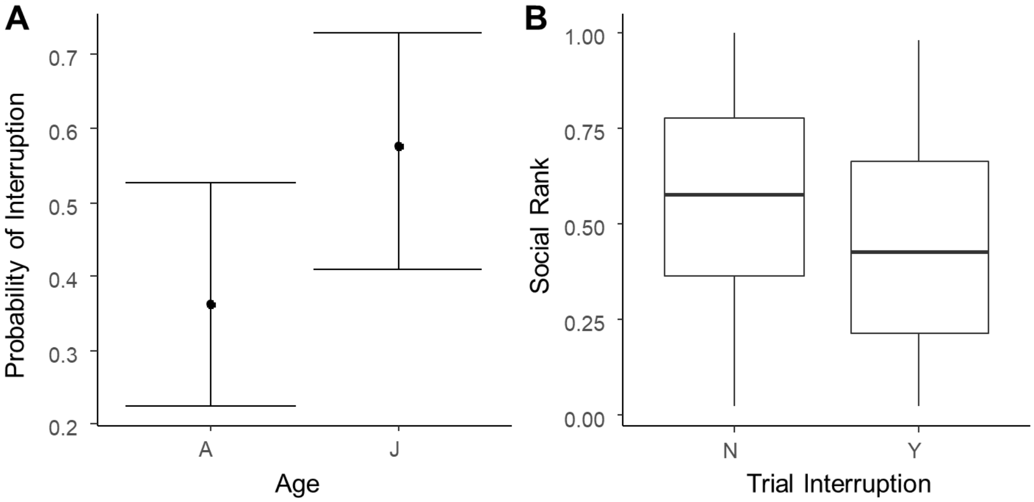

Figure 8.2 Individual differences in the likelihood of being interrupted by conspecifics in an associative learning task with coloured kernels (N = 38). (A) Probability of being interrupted depending on individual age (A, Adult; J, Juvenile); and (B) Boxplot of the occurrence of an interruption (N, No; Y, Yes) depending on individual social rank (0-1, lowest to highest rank). On the left plot (i.e. plot A), dots indicate the mean probability of interruption and error bars represent 95% confidence intervals. On the plot on the right (i.e. plot B), the horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values.

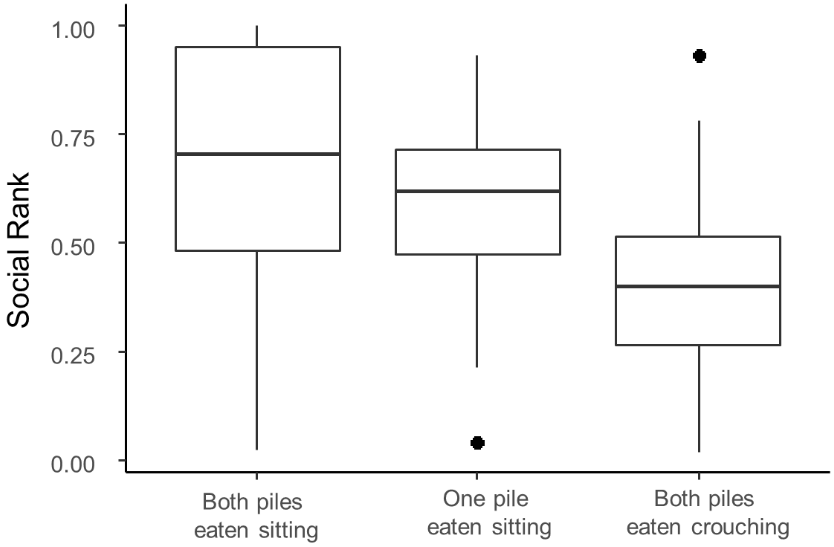

Figure 8.3 Boxplot of the physical positions individuals adopted in the associative learning task involving coloured corn (N = 38) based on their social rank, ordered from the least surreptitious (left) to the most surreptitious (right) technique. The horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

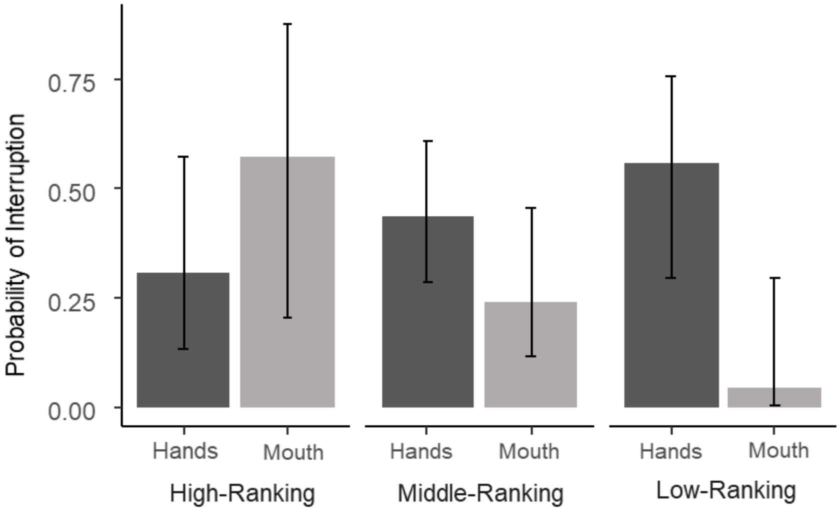

Figure 8.4 Individual differences in the probability of interruptions in an associative learning task with corn (N = 38), according to the mechanical behaviour used and social rank. Social rank was analysed as a continuous variable but for graphical purposes, plotted here using the highest (“high-ranking), median (“medium-ranking”) and lowest (“low-rank”) ranks of the sample. Error bars represent 95% confidence intervals. Mechanical manipulations were classified as either eating both piles of kernels with their hands, or eating one or both piles directly with their mouth.

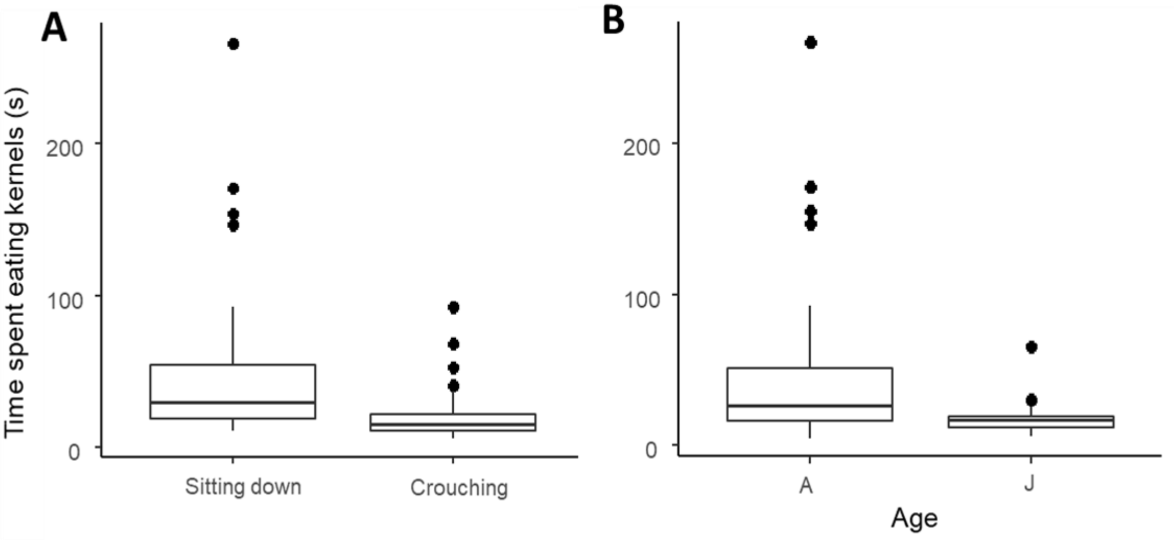

Figure 8.5 Individual differences in the time spent eating foot items in an associative learning task involving coloured corn kernels (N = 38). (A) boxplot of the time spent eating and the posture adopted while doing so. (B) boxplot of the time spent eating relative to age (A, Adults; J, Juveniles). The horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

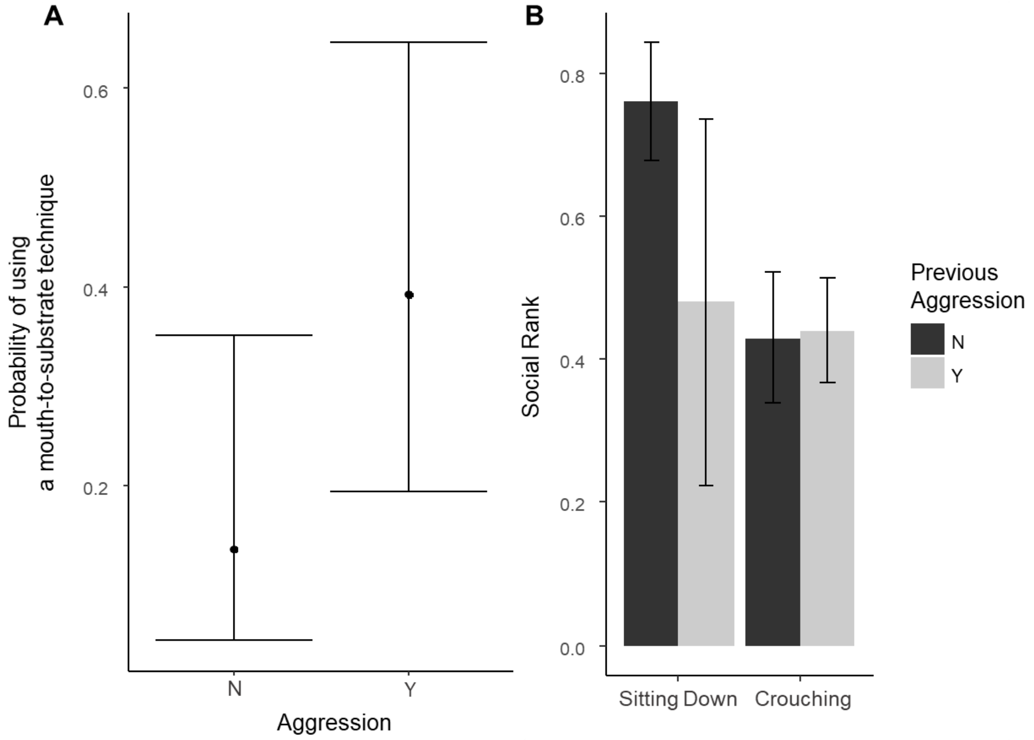

Figure 8.6 Individual differences in the use of foraging techniques in an associative learning task involving coloured corn kernels (N = 38). (**A**) probability of using an inconspicuous mechanical manipulation to eat the corn kernels according to whether or not individuals received aggressive interruptions in the previous trial (Y, Yes; N, No). (**B**) barplot of individual physical positions according to social ranks and whether or not those individuals were recipients of aggressive interruptions in the previous trial (0, No; 1, Yes). On the left plot (i.e. plot A), dots represent the mean probability of using a mouth-to-substrate technique. Error bars represent 95% confidence intervals.

8.4.2 Associative Learning Task 2

In this task, I tested 27 individuals over 81 trials that included the presentation of corn kernels. There were no differences in the mechanical manipulation used, as individuals always used both hands to eat the pile of corn kernels in all trials. However, on 23 occasions (40% of trials), individuals ate the kernels crouching instead of sitting down (34 cases, 60%). Animals ate the kernels in a median average of 12.5 s (range: 0-46 s).

In this task, I found no evidence to support my first, third and fifth hypotheses: I failed to obtain a minimum-adequate model for H1 or H3, and the only significant predictor in H5 was dominance rank (lower ranked animals were more likely to use an inconspicuous physical position, irrespective of aggression in the previous trial, Table 8.3, $MT2_{Prev}$). However, I did find more support for hypotheses H2 and H4 in this task. In line with my second hypothesis, low-ranking individuals were more likely to crouch whilst eating the kernels (Table 8.3, $MT2_{Tech}$, Fig 8.7A); and in line with my fourth hypothesis, crouching individuals eat faster than those sitting down irrespective of age or rank (Table 8.3, $MT2_{Un}$, Fig 8.7B). See Table 8.5 for a summary of all results.

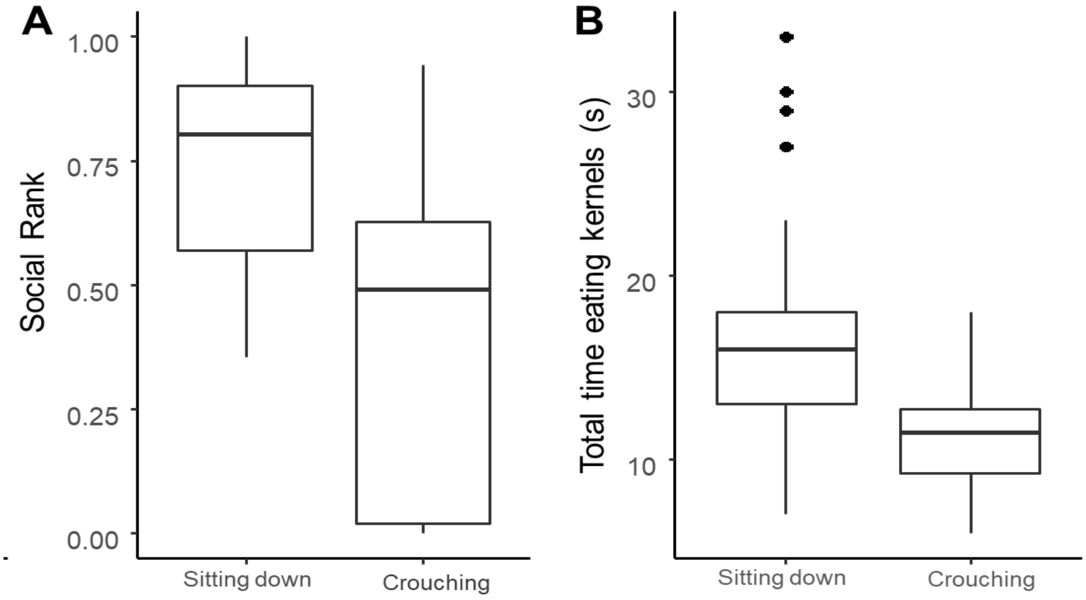

Figure 8.7 Individual differences in the exploration given to a second-order conditioning task (N = 27). (**A**) Boxplot of the social rank of individuals and their physical position whilst eating. Rank varies from 0-1 (lowest to highest rank); (**B**) Boxplot of the time individuals spent eating the kernels and their physical position. The horizontal line in each box indicates the median, the box shows the lower (25%) and upper (75%) quartiles of the data, and the whiskers the minimum and maximum values. The dots indicate outliers.

Table 8.5 Summary of results obtained relative to the hypotheses tested.

Hypothesis	Task	Response	Model	Observed Effects	Support
H1	1	Occurrence of interruption (Yes/No)	$MT1_{Vul}$	Age Social rank	Full
	2	Occurrence of interruption (Yes/No)	$MT2_{Vul}$	–	None
H2	1	M. Manipulation	$MT1_{MTech}$	Age (*p*=0.055)	Partial
	1	P. Posture	$MT1_{PTech}$	Social Rank	Full
	2	M. Posture	$MT2_{Tech}$	Social Rank	Full
H3	1	Occurrence of interruption (Yes/No)	$MT1_{Int}$	M. Manipulation*Rank P. Posture*Age (*p*=0.05)	Partial
	2	Occurrence of interruption (Yes/No)	$MT2_{Int}$	–	None
H4	1	Time spent eating kernels	$MT1_{Un}$	M. Manipulation (*p*=0.05) P. Posture Age	Partial
	2	Time spent eating kernels	$MT2_{Un}$	P. Posture	Partial
H5	1	M. Manipulation	$MT1_{MPrev}$	Previous Interruptions	Full
	1	P. Posture	$MT1_{PPrev}$	Previous*Rank	Partial
	2	P. Posture	$MT2_{Prev}$	Social Rank	None

Overview of the results relative to each of the hypotheses under test. Shown are: (*i*) the hypothesis references; (*ii*) the task reference 1, associative learning task 1; 2, associative learning task 2; (*iii*) the response variable used in each mode; (*iv*) the name of each model; (*v*) the main effects or interactions that were significant in each model; (*vi*) the support found for each hypothesis.

8.5 DISCUSSION

In this chapter, I analysed the foraging techniques of individuals from two groups of wild chacma baboons used during two cognitive assessments involving food items. I used differences in two aspects of foraging technique, namely mechanical manipulations and physical postures, to evaluate five hypotheses. In most cases, I obtained at least partial support for the hypotheses under test. However, there are two important caveats. First, that the support obtained was much more consistent for task 1 than for task 2. Second, if we focus primarily on task 1, I only obtained full support in 2 of 5 cases, indicating that we need to nuance in our interpretation of the support for these hypotheses. I will consider these two caveats in turn.

In the first case, the most probable explanation for the stronger support in task 1 is that this task was considerably longer and involved double the food reward – consequently, the baboons had more to lose, and more time in which to lose it, making the observed effects on vulnerable individuals (H1, H2), the advantages of the different techniques (H3, H4), and the response to previous aggression (H5) that much more marked in this task. Moreover, it’s possible that the difference in food amount between the tasks determined the occurrence of interruptions, as having twice the amount of food in the associative learning task 1 likely increased the chances of being interrupted mid-trial. This may reflect why in the associative learning task 1 but not in the associative learning task 2, I found full or partial support for H1, H3 and H5, as all of these hypotheses evaluated, in one way or another, the relation between aggressive interruptions and vulnerable individuals. At the same time, evidence for H2 and H4 was found in both tasks likely because they reflect common techniques used by vulnerable individuals to consume valuable food items. In the second case, I found a mostly consistent effect of social rank across my results in the associative learning task 1. Providing partial support for four out of the five hypotheses, social rank predicted, the likelihood of being interrupted; the use of a surreptitious behaviour; the use of an inconspicuous behaviour to avoid trial interruptions; and the use of an inconspicuous behaviour in response to previous aggression. These results suggest that animals of low-rank are generally vulnerable to conspecifics and may actively avoid interruptions by adopting inconspicuous behaviours that allow them access to resources. It's possible some of inconsistencies between the effects of age and social rank arose because both effects were difficult to differentiate from one another. Studies in this population show that juveniles are tolerated to join foraging patches even when animals of higher-ranks are occupying them (Lee & Cowlishaw, 2017); however, adult subordinates are not able to do the same. Moreover, juveniles' access to resources, can be facilitated by the presence of their mother or siblings, particularly in the case of high-ranking kin, who help establish juveniles' rank (Lea et al., 2014). Thus, it is impossible to know whether the behaviour of juveniles in this study was affected by the proximity (albeit out of sight) of their kin or whether it was truly an effect of their rank.

As postdicted in in my first hypothesis (H1), juveniles and low-ranking animals were more likely to be interrupted during a task, albeit this was observed only in the associative learning task 1. This was perhaps unsurprising, as low-ranking (Abbott et al., 2003) and juvenile (Bernstein et al., 1983) individuals commonly have high rates of aggression directed at them; while additionally in the former case, individuals are often constrained from exploiting food patches (Lee & Cowlishaw, 2017). At the same time, I found partial support for my second hypothesis (H2), as low-ranking individuals were more likely to adopt inconspicuous postures whilst foraging in both tasks. These results suggest vulnerable individuals may adopt inconspicuous postures to limit the amount of information conspecifics aggressively respond to and likely use to interrupt foraging bouts (i.e. producer-scrounger: Giraldeau & Caraco, 2000). Indeed, partial support my for my third hypothesis (H3) suggests this may be the case, as low-ranking animals were able exploit valuable food items provided in the associative learning task 1 by using an inconspicuous manipulation that allowed them to avoid interruptions from dominant conspecifics. The use of different foraging behaviours by vulnerable individuals is not uncommon. For instance, low-ranking animals can develop different diets in order to avoid proximity with their dominant conspecifics (Murray et al., 2006). Juveniles too, forage separately from their adult conspecifics, often encountering novel food items which adults ignore (Cambefort, 1981). Cognitive studies have likewise found vulnerable individuals to change their behaviour to avoid aggression from conspecifics. For example, Drea et al. (1999) reported low-ranking macaques “played-dumb” in the presence of dominants, seemingly performing poorly when tested in a group setting to avoid aggressions, but not when tested on their own.

In both, the associative learning task 1 and the associative learning task 2, adopting a crouched posture whilst eating the kernels allowed individuals to eat more quickly during the uninterrupted trials. The latter confirms my initial postdictions that animals would be more likely to adopt a technique which would allow them to eat efficiently (H4). As mentioned previously, it’s possible that crouching over the kernels limits the distance from the substrate to the mouth, allowing individuals’ to eat the foods more quickly than if they were sitting down. At the same time, eating the reward more quickly in the case of juveniles, may reflect the natural feeding behaviour inexperienced individuals (i.e. Gochfeld & Burger, 1984) rely on to exploit the food items they have access to at this stage. Because the corn kernels required no technical experience with which to exploit them, it is possible juveniles ensure success by eating the rewards quickly. Alternatively, the motivation to consume food items quickly may be more pronounced in juveniles, as they are commonly restricted in their access to resources. Unfortunately, it is difficult to distinguish between both of these alternatives. In addition to using mechanical manipulations or physical postures to eat food items more quickly, baboons have another means by which they can eat considerable amounts of food in a short amount of time. Chacma baboons, like other Old World Monkeys, have cheek pouches which they use to temporarily store food (Hayes et al., 1992; Smith et al., 2008). Research has shown that the use of cheek pouches increases when resources are clumped (Lambert & Whitham, 2001), when foraging on valuable food items such a fruits (Hayes et al., 1992; Lambert, 2005), and when the rank of the nearest neighbour increases (Smith et al., 2008). While I was unable to measure cheek pouch use in the experiments due to the small amount of kernels provided (there was no discernible growth in the pouches due to food storing), it is possible individuals in both associative learning tasks stored kernels in their food pouches, allowing them to collect the kernels faster.

Following my postdictions for my fifth hypothesis (H5), individuals were more likely to use inconspicuous behaviours in the associative learning task 1 after being recipients of aggressive interruptions. Specifically, individuals were more likely to use the mouth-to-substrate technique regardless of their phenotype/state; while animals of lower rank were more likely to eat the kernels crouching after aggressive interruptions. One possible explanation for such results may be that because animals were interrupted whilst using a conspicuous technique (i.e. using both hands to eat/sitting down), they would be more likely to avoid using such technique in the future as it's now associated to a negative event. Another possibility for using such a technique, may be explained by motivational differences, as animals who lost a valuable reward in the previous trial may be more likely to use inconspicuous techniques to prevent further loss of food items. My current hypothesis and analysis did not consider whether animals changed techniques between each presentation due to interruptions; however, one way to test the suggestions described above, would be to evaluate the technique used at the time of the interruption and compare it to the one used in the following food presentation. A possible reason for why there was a rank-dependent effect with regards to the use of inconspicuous postures may be because animals of low-rank commonly such behaviours (see: H2) and so, are more likely to adopt these techniques after being interrupted.

One point which remains to be addressed is whether the use of inconspicuous behaviours could reflect a genuinely deceptive behaviour or a learned response by the individuals that practice such behaviours. According to Byrne & Whiten (1992), deception is defined as those acts that deviate from a normal set of behaviours, such that conspecifics misinterpret their intention. A number of studies show that individuals employ a variety of behaviours which could be classified as deceptive to avoid social conflict over contested resources, such as hiding food behind opaque objects to avoid raiding from conspecifics (ravens, *Corvus corax:* Bugnyar & Kotrschal, 2002) or adjusting their foraging behaviour in the presence of conspecifics (*C. corax*: Heinrich & Pepper, 1998). There are plenty of such observational examples regarding the *Papio* and *Pan* genera (e.g. Byrne & Whiten, 1992). However, empirical evidence on "true" deceptive behaviours has so far been scarce, as such tactics work best when rare (Hall & Brosnan, 2017). In Chapter 5, I detail how juveniles and low-ranking animals were more likely to move the coloured bags away from where the area where they were first presented. Similar behaviours have been observed during other experimental primate studies, and while they have not been referred to as deceptive, they follow the logic that animals are aware of what conspecifics know and act accordingly to avoid aggression. For instance, Hare et al. (2000) reported subordinate chimpanzees commonly chose food items that dominants could not see, and in some cases hid or waited to get a reward even when it meant losing the most valuable piece of food. However, while the behaviours observed in Chapter 5 follow what has previously been termed as deceptive tactics (e.g. Bugnyar & Kotrschal, 2002), I limit myself to describing the techniques evaluated in that Chapter or in the current one as "deceptive", as it is difficult to ascertain the intentionality of such techniques and I am unable to confirm this one way or another. However, irrespective of whether or not there is attribution of mental states, my results suggest that vulnerable animals employ inconspicuous foraging techniques to lower the risks of losing valuable foods to adult and/or dominant animals. It’s possible that to some degree, individuals recognize the sort of behavioural cues that alert conspecifics to the presence of valuable foods, likely because they themselves have exploited such cues in the past (albeit non-aggressively).

If adopting a technique, such as eating with the mouth directly is both, more inconspicuous and quicker than picking-up kernels with the hands, then why do animals employ other techniques? One possible reason why the foraging technique adopted by individuals varied within and between tasks may have to do with the trade-offs between adopting a time-consuming technique versus a fast-technique. For instance, whilst the mouth-to substrate technique eliminates any visual cues involving the movement of arms, it may not afford individuals time to investigate the quality of food. Chacma baboons in this population have often been observed to rub food items on their fur, presumably to clean them of sand (pers. obs; for an example in yellow baboons, see Rhine & Westlund, 1978). Additionally, in the associative learning task 1 the corn presented had been made unpalatable with a bitter substance, perhaps requiring more exploration than usual. Moreover, while inconspicuous behaviours likely decrease the chances of being interrupted, adopting such techniques may present ecological and/or social costs to individuals who use them. For instance, crouching or using a mouth-to substrate technique requires individuals to lower their head whilst eating, constraining their view and forcing individuals to stop eating in order to lift their heads and scan their surroundings. Such trade-offs are often highlighted in the predator avoidance literature (e.g. Cowlishaw et al., 2004; Ebensperger et al., 2006), but social vigilance involves the same trade-offs, as vigilance of any sort is often difficult to perform at the same time as other activities (Fernández-Juricic et al., 2005; Kutsukake, 2007).

In this study, I found state-dependent variation in foraging techniques used whilst participating in two cognitive tasks involving corn kernels. In the case of the associative learning task 1, I find full support and partial support for two (H1 & H5 respectively) of the five hypotheses proposed; while in the case of the associative learning task 2, I find full and partial support for two (H2 & H4 respectively) out of five hypotheses. Inconspicuous foraging techniques were found to be predominantly rank-dependent, as low-ranking animals were more likely to use inconspicuous techniques that limited their exposure to conspecifics, likely reflecting the manner in which poor competitors obtain valuable resources. However, given that this study was based on postdictions, independent replication must be conducted to provide robustness. While other underlying causes may drive animals to use a given technique, such as maternal effects (van Schaik et al., 2003) or environmental changes during ontogeny, cognitive tasks may still provide researchers with an reliable scenario in which to quantify foraging behaviours.

Chapter 9

Discussion

Understanding individual differences in cognition is important because variation in cognition may bring about differences in fitness. Additionally, focusing on the variation within a population could improve our knowledge of how cognitive traits develop and are selected for in a given species, for a given ecosystem. Research has recently turned its attention to the individual differences found in cognitive abilities; however, while the need for testing such variation in wild settings has been recognized, most studies are still restricted to captive conditions. The aim of this thesis was to measure variation in cognitive abilities in wild chacma baboons by testing individuals with three associative learning tasks: two operant conditioning tasks (one involving coloured corn kernels that differed in taste, the other involving coloured paper bags that differed in reward) and a second-order conditioning task. At the same time, I evaluated whether individuals' phenotypic traits and/or states influenced cognitive performance in the two operant conditioning tasks. Additionally, using individuals' behaviour during testing, I evaluated two aspects of individual variation that may affect task performance but are rarely taken into account in studies of cognition: individuals' motivation to approach and solve a task, and how individuals interact with the tasks' food rewards. In this final chapter, I discuss some of the main findings of my work, some of the variables that possibly determined the baboons' performance in the cognitive tasks, and the importance of testing wild animals in cognitive studies.

9.1 INDIVIDUAL VARIATION

Across the three associative learning tasks, my findings suggest that the baboons generally failed to learn the associations as intended. However, in the two tasks where I was able to explore individual variation in learning ability and its correlates, I did find some evidence of phenotype-related variation in task performance. Specifically, in the task involving coloured bags, there was some evidence of learning within a subset of individuals according to their personality and sex (see Chapter 5). In addition, the social rank and age of individuals were determinants of both individuals' participation in the tasks and foraging techniques used to eat the food rewards provided (see Chapters 7 & 8 respectively). Finally, sex was also found to determine individuals' motivation to participate (Chapter 7). Below, I discuss why I was unable to find more evidence of individual variation in associative learning, and the potential implications of individual variation in task participation/foraging techniques on animal cognition research.

9.1.1 Individual Variation In Learning Ability

One possible contributor to the baboons' failure to learn the intended associations in the cognitive tasks, and thus to show individual variation in learning ability, may have been the prevailing environmental conditions the baboons experienced at the time of testing. I explore this possibility further below. Another possible explanation for why learning, and individual variation in learning, was only observed in the coloured bags task may have to do with the nature of the task itself. Out of all the tasks implemented, this was the most appropriate one as it had the right balance of novelty and a reward. In the first task presented, for example, animals not only ate the majority of kernels whether bitter or not, but immediately approached the task and had very low levels of exploration throughout. In contrast, the third task presented provided no food reward for a significant part of the task with which to motivate the animals to approach and interact with the task. The task involving the coloured bags, on the other hand, presented individuals with two novel items, which required individuals to open each bag, rather than seeing directly, to find the reward. As a result, it is possible that those individuals who were more likely to be conservative towards novelty, such as shy animals (Sih & Del Giudice, 2012) and females (Hopper et al., 2014), as well as more motivated by the reward, were more likely to explore the correct bag more after several presentations.

Overall, my results regarding individual variation in cognitive abilities perhaps reflect the difficulties in providing animals with a task that captures such variability whilst avoiding sample biases resulting from individual differences in participation or current environmental conditions. One of the main difficulties in this study was finding suitable tasks with which to test the baboons, as common testing apparatuses previously used to test primates (e.g. Manrique et al., 2013; Schmitt et al., 2012) were inappropriate for tests in this population. First, stationary testing apparatuses, which are frequently adopted in captive settings (e.g. Fagot & Bonté, 2010), would have likely been monopolized by dominants and allowed social learning by others observing the dominant animals before they were individually tested. Second, more complex tasks (e.g. van de Waal et al., 2013), would have likely required a longer time to solve, increasing the likelihood of interruptions and/or number of witnesses. These points were relevant to consider, as avoiding the spread of social information was key for the purposes of this research. As previously detailed in Chapter 2, many captive studies benefit from the use of complex testing apparatus and allow longer periods of time to solve each task. Such differences suggest that standard laboratory tests which assess individual variation are, for the most part, not applicable to the wild, or at least for many social species.

Associative learning tasks were chosen as the focus in this study not only because they represent a widespread and important cognitive process, but because they made it possible to test each baboon separately and repeatedly whilst quantifying individuals' differences. However, a combination of potential complications, including environmental conditions, task design (that appropriately balances novelty and reward), and unanticipated methodological issues in all three tasks—specifically the acceptance of the bitter kernels, despite preliminary tests that showed an aversion to the bitter substance (task 1); the continuous sampling of each bag (task 2); and the lack of attention to the stimuli (task 3)—meant that the tests were less effective than intended at facilitating the baboons to learn the planned association.

9.1.2 Individual Variation In Motivation And Foraging Techniques

Motivation to participate in both the coloured bags and second-order conditioning tasks was determined by three phenotypic traits: age, social rank and sex. The most robust result was the age effect; juveniles were more motivated to participate in each task by having either lower latencies to approach the task, higher exploratory rates of the task, or both (Chapter 7). Similarly, age and rank were determinants of the foraging techniques used by the baboons to eat the food rewards offered in each task; juveniles and low-ranking animals were more likely to use techniques that were less conspicuous and allowed faster consumption of the rewards, which alone or in combination led to a lower rate of interruptions (Chapter 8).

Understanding the differences in individuals’ participation and foraging techniques in this thesis was done partly with the objective of addressing possible sample biases in cognitive testing. Participation, trial interruptions and the efficiency with which animals consume food rewards will likely determine the data that are analysed, as well as the conclusions drawn from those results. My findings suggest that more vulnerable animals should not only use more efficient foraging techniques to consume as much as possible before an interruption (Chapter 8), but be more motivated to participate in a task because their relative payoff of a high-value food reward is larger for them compared to conspecifics who normally have priority-of-access to food resources (Chapter 7). While these two aspects of individual variation are usually controlled for in captivity—by restricting food prior to testing in the case of motivation and/or testing animals outside of their conspecific group to avoid interruptions—studies in the wild are unable to do this. Having long-term behavioural data, as well as robust knowledge of the demographics of the population under study, may help avoid biases in wild settings. For example, not having information on the social position of individuals prior to testing, may inadvertently bias a sample towards low-ranking individuals who are more likely to participate. As more cognitive studies are carried out in wild conditions, I would recommend that future studies consider and report adequately on these issues, and consider their potential impacts on sample bias, when drawing conclusions about individuals' task performance.

9.1.3 Individual Variation In Relation To Stress

Although both acute and chronic stress may influence cognitive performance (Joëls et al., 2006), as well as patterns of task participation and foraging techniques, I was only able to consider the effects of acute stress on patterns of task participation (for the second-order conditioning task only, Chapter 6) in this study; however, my analysis of these patterns yielded no relationship between stressors and task participation, likely because I lacked sufficient observations. Since I relied on behavioural observations (Ellis et al., 2011), I measured short-term stressors in the focal follows prior to each trial; however, due to the continuous competition for resources, be it food, mating or grooming partners, it is possible some individuals' (i.e. low-ranking animals: Abbott et al., 2003) participation was more likely to depend on chronic stressors rather than acute ones, as the persistent activation of the stress systems that impair cognitive performance (Luine et al., 2007), could similarly affect individuals' motivational states. A productive future research direction could be to determine how cognitive performance is affected by acute and chronic stress responses (as well as how these vary between individuals), by including behavioural observations as well as faecal glucocorticoid analysis, which may be best for measuring long-term stress responses.

9.2 BABOON COGNITION

Certain behavioural and ecological traits of the species under study may have affected individuals' performance and variation (as well as their participation and feeding techniques) in each of the tasks presented. In the following section, I consider some of the ecological and social characteristics of the study population that may have influenced the results obtained in this thesis, including how different populations of chacma baboons could compare with each other. I additionally discuss some aspects of chacma baboons' cognitive behaviour that may commonly influence their task performance.

9.2.1 Current Environment

The results of the coloured kernels and coloured bags tasks (Chapters 4 and 5 respectively) suggest that baboons prioritize repeated exploration of each task over, or in spite of, learning. In unreliable conditions where resources are patchy, animals may prefer to constantly sample and update their information. A mitigating circumstance of the studies in this thesis were the ecological conditions individuals were experiencing at the time of testing; in the following sections, I not only discuss the potential role the physical environment had on task performance, but additionally touch on the potential effects of the baboons' social environment and consider some potential cognitive differences between baboon populations distributed across Southern Africa.

Physical environment

Studies have often found that individuals from variable habitats outperform conspecifics from stable habitats in cognitive tasks (e.g. Roth et al., 2010; Schwarz & Cheng, 2010; Tebbich & Teschke, 2014). Such studies, however, have worked on the basis that the conditions of an environment, although unfavourable, are consistent over time. Based on this, it is unclear how cognitive processes develop in environments that suffer marked changes over shorter periods of time (i.e. within-generation predictability: Dridi & Lehmann, 2016). The theoretical literature suggests that learning about novelty is not preferred in heterogeneous environments where resource abundance varies (Kerr & Feldman, 2003; Niemelä et al., 2013). We know that the Tsaobis environment, while predictably seasonal, can have years of exceptional resource abundance followed by years of intense drought. Moreover, research in other populations of baboons shows that baboons have an episodic-like memory (i.e. events that occur in the same circumstances only once) and are able to remember whether a source of food has been previously depleted (Noser & Byrne, 2015). This raises the question of whether chacma baboons living in heterogeneous and often unpredictable environments always learn relevant associations involving stimuli in their environment. One possible explanation of my findings may be that, in favourable times, cognitive abilities such as associative learning are promoted by the abundance and reliability of resources; while in unfavourable times, such as the period of this study, animals use past information that applies to known resources, but continuously sample novel stimuli. If the baboons’ performance was indeed affected by the difficult conditions in which they were tested, then it is possible different results would be observed in a year where the abundance of resources was better predicted.

Another possibility is that learning may be dependent on the most salient cues at a given time (Shettleworth, 2010) and the baboons learnt to associate an unintended but more salient cue with the food reward in my experiments. In harsh conditions, relevant traits associated to cues, such as spatial location, quantity, nutritional value and/or accessibility, may be better reinforcers of an association because they will provide a higher payoff. For example, greenfinches (*Carduelis chloris*) favoured salient coloured cues to locate food in a one-trial test after an initial presentation, but favoured spatial cues after receiving repeated presentations of the same task (Herborn et al., 2011). In the case of the baboons, although food rewards were presented in each task, the cues provided may not have been salient in the way that was expected. For instance, it was predicted that the bitterness of the kernels and the non-rewarding pebbles would deter individuals from choosing those options in the coloured kernels (Chapter 4) and coloured bags (Chapter 5) experiments, respectively. However, perhaps the salient cue in each task was that the presence of coloured kernels or bags signalled the presence of a reward regardless of taste or content. This seems to be particularly true in the case of the coloured bags, as there was no large cost in exploring both bags repeatedly and in most cases the reward was still obtained.

The degree to which the current physical environment and availability of food resources affected individuals' use of information in each task is difficult to estimate with my current data.

Social environment

Individuals' performance may not be limited only to changes in their physical environment, but to their social one as well. Studies with lemurs (*Varecia variegata* and *Varecia ruba*) for example, report that differences in innovation and social learning depend on the sex ratio of the group (Dean et al., 2011). Social instability at the time of testing, in particular that involving adult males (Bergman et al., 2005; Creel, 2001), may likewise affect cognitive performance by altering individual levels of glucocorticoids, which in turn are known to impact cognitive ability (i.e. Bergman et al., 2005). One of the years during which the baboons were tested (2016) was characterised by significant social instability, as evidenced by a preceding fission event in one troop and an unstable male hierarchy in the other (C.M., personal observation). It is possible such instability, exacerbated by the prevailing drought and the increased competition for resources, affected how individuals in each troop responded to the tasks. While my study does not investigate this directly, it is possible the impacts of the social environment on individuals did not align with the traits/states under evaluation and as a result, may have confounded my analysis on those traits.

Comparisons between populations

The effect of the current environment, physical or social, on task performance in this population could be tested by performing experiments in these groups at different times to capture this variation. However, another productive avenue could be to compare populations across multiple years. There are plenty of cases in which populations from the same species exhibit different cognitive behaviours due to their divergent experiences in habitats with unique socio-ecological challenges (e.g. Burns & Rodd, 2008; Krützen et al., 2005). For example, Pravosudov & Clayton (2002) reported that black capped chickadees (*Poecile atricapilla*) from environments with limited food resources performed better in a spatial learning task than conspecifics from an environment with a stable abundance of resources. Since chacma baboons are widely distributed across Southern Africa, proliferating in diverse habitats which include deserts (Hamilton, 1986), savannahs (Cheney & Seyfarth, 2007) and urban landscapes (Fehlmann et al., 2017), it is possible that different populations would respond differently to the same stimuli according to the challenges of their specific environment. For example, because anthropogenic resources are likely to be reliable and highly energetic, cognitive processes such as learning and spatial memory are more likely to be promoted in animals living in urban environments (Barrett et al., 2018; Griffin et al., 2017).

9.2.2 Information Acquisition And Use

We currently depend on individuals' use of information to define and measure cognitive abilities, often assuming that if a given piece of information was successfully collected and processed, it must be applied as expected. Such an assumption may be unwarranted however, and raises the question of whether the failure to use information as expected is due to a failure to learn or another reason (Carter et al., 2016). In the case of one of the associative learning tasks presented here (coloured kernels, Chapter 4), for instance, it is possible that the test subjects learnt the difference between the stimuli, i.e. that one colour was bitter while the other was not, but because they were largely unaffected by the bitterness they did not use this information as expected (i.e. that eat all the kernels, rather than leaving the bitter kernels uneaten). Similarly, low-ranking animals may avoid aggression by ignoring rewards about which they have spatial and visual information (e.g. Hare et al., 2000), which may involve “playing dumb” (Drea & Wallen, 1999). Such behaviour could have occurred in my study, limiting individuals’ participation and performance in the tasks, but not representing the knowledge of the individuals. While the previously listed studies actively investigated the relationship between information acquisition and its subsequent use, it is possible that other studies have underestimated the cognitive abilities of animals because those animals failed to use information as expected due to their current circumstances.

9.2.3 Behavioural Flexibility

The variability of the environment, as well as the reliability of the resources in it, are important drivers of cognitive abilities (Niemelä et al., 2013). Behavioural flexibility allows animals to adjust their behaviour according to the current environment, requiring individuals to apply past information to novel situations and/or to develop behaviours to solve novel problems (Godfrey-Smith, 2001; Logan, 2016). It is possible that chacma baboons did not show evidence of learning in my experiments because they are a behaviourally flexible species. In other words, by definition, flexible animals should be able to respond to stimuli optimally in relation to their current environment (Niemelä et al., 2013), and this may require individuals to constantly update their information about the environment, masking any evidence of associative learning. Chacma baboons commonly exploit a wide array of food sources (e.g. Hamilton, 1986). Likewise, baboons are able to change their daily behavioural and dietary patterns to compensate for injuries (Beamish & O’Riain, 2014) and change their time budgets depending on the environment in which they forage (Fehlmann et al., 2017). It is because of their dietary and behavioural flexibility that chacma baboons are such a successful species, surviving in a wide number of habitats ranging from harsh arid environments, such as the pro-Namib Desert, to urban landscapes where anthropogenic resources can be easily exploited (Beamish & O’Riain, 2014; Fehlmann et al., 2017). Being behaviourally flexible may allow baboons to learn about relevant stimuli in their current environment but may make them a difficult species in which to test for evidence of associative learning.

9.2.4 Conservation Impact

The process of urbanization has caused drastic environmental changes at such fast rates, some species are unable to adapt (Greggor et al., 2014; Sol et al., 2013); yet, others have taken advantage of such environments and the resources within, by adjusting their behaviour in response to novel, anthropogenic stimuli. Chacma baboons, in spite of the expansion of urban areas across Southern Africa, are a thriving species, largely due to their raiding of anthropogenic resources (Fehlmann et al., 2017). Such success is not without consequences however, as raiding behaviour poses a risk to baboons and puts them in constant conflict with humans. Recently, conservation efforts have turned to cognitive mechanisms to address and mitigate human-wildlife conflict (Greggor et al., 2014, 2017). Cognitive mechanisms such as learning, can give insight into how animals cope with anthropogenic changes, as it allows animals to adjust their behaviour when they encounter novel situations. For example, operant conditioning has been proposed as a possible strategy with which to mitigate the negative impact of roads on wildlife (Proppe et al., 2017). Nuisance species such as chacma baboons, are believed to have greater levels of neophilia and to be behaviourally flexible, which facilitates habituation and greatly contributes to their success (Barrett et al., 2018; Sol et al., 2002); yet, so far, there has been little research into harnessing learning mechanisms to manage such species. The work described in this thesis, while far from being a conservation plan, does provide significant information as to the sort of cues baboons do and do not respond to, as well as potential time frames in which baboons could develop relevant responses. These two aspects, along with the considerable knowledge regarding the spread of novel information through the social system (e.g. Carter et al., 2015) could be used to develop a long-term management strategy for chacma baboons.

9.3 CAPTIVE AND WILD SETTINGS

Currently, the study of cognition is strongly biased towards captive testing, where the results obtained are commonly generalised to wild populations. However, it is clear that captive animals experience almost every aspect of their lives differently to their wild counterparts, from the food they consume to the stimuli to which they are exposed (Mason et al., 2013). In Chapter 2, I established some of the most relevant differences between cognitive studies in captive and in wild settings. Throughout this thesis, too, I have discussed such differences in relation to the methodology and results observed in my own cognitive tasks. Nevertheless, there are additional aspects of captive testing that may affect how cognitive abilities develop in captivity compared to the wild. Since the results found in captivity are commonly interpreted to represent a species' cognitive repertoire, it is important to address these additional aspects, because they may explain why captive and wild studies often differ in their findings.

9.3.1 Testing Stimuli

Much emphasis has been put on the significance of the stimuli used in cognitive testing, as animals will be more likely to respond to stimuli that are ecologically relevant to them. However, the saliency of these stimuli will differ in important ways for captive and wild animals, and these differences are frequently overlooked. For example, captive animals may have only been given ripe fruits to eat, compared to wild conspecifics who witness changes in fruit maturation (Regan et al., 2001). The results of my first experiment (coloured kernels, Chapter 4) suggest that the baboons failed to demonstrate they had learned the colour-taste association because the bitterness of the kernels was insufficient to deter them from eating what was otherwise a highly nutritious food. In contrast, animals in captive settings are often provided from an early age with preferred foods *ad libitum* (Zandberg et al., 2016) and may be more responsive to differences between palatable and unpalatable foods used in testing.

Similarly, captive animals may be exposed to a variety of anthropogenic objects characterized by features that differ greatly from what their wild counterparts are exposed to (Mason et al., 2013). Indeed, there is evidence that captive animals develop abilities that are not observed in their wild conspecifics due to their high exposure to anthropogenic stimuli (Haslam, 2013). The sorts of cues that animals find meaningful and to which they respond throughout their lives may ultimately determine the cognitive abilities that they develop. Given the differences between captive and wild settings, these would be very different for captive and wild animals. It is thus important for captive studies to ensure animals are reared in environments that simulate their natural habitat and later test animals with stimuli and/or conditions typical of this environment or to address such differences rather than indiscriminately generalising the results to wild populations.

9.3.2 Testing Regime

One of the reasons why testing cognitive variation in wild animals is so challenging is because cognitive evaluations require repeated measures of individuals. While repeated testing has been made possible by using automated or stationary devices that allow the collection of hundreds of testing instances (e.g. Franks & Thorogood, 2018; Morand-Ferron et al., 2015), this may be a potential source of bias, as some individuals can be restricted in their access to the apparatus (e.g. Jones et al., 2017); show motivational differences to engage with it (e.g. van Horik & Madden, 2016); and/or obtain social information about it by observing conspecifics interacting with the task. In addition, for most natural stimuli, it is unclear whether wild animals would encounter these at such high rates, considering that the abundance and distribution of a given novel stimulus about which an individual could learn will be dependent on the nature of the stimulus and the environment. These points are not only limited to associative learning, but may also be relevant when testing more cognitively complex abilities, such as problem-solving or tool-use. This type of discrepancy further challenges the validity of generalising results from captivity to understanding cognition in the wild.

There is one other point to raise about the numbers of re-tests in captive experiments. The three cognitive assessments described in this thesis consisted of relatively few trials per individual, partly because of logistical constraints, but also due to a trade-off between the number of individuals that could be tested and the number of trials that could be conducted per individual. Given that my aim was to evaluate individual differences, I decided to focus on the former to ensure a variable and representative sample. However, in many cognition studies, the opposite decision is made, and fewer individuals are tested many times. This further limits the generalisability of the results of many studies in captivity, as smaller samples are less likely to be representative. Trade-offs such as these are a common challenge for cognition researchers; however, properly understanding individual variation is likely to require larger samples of individuals.

9.3.3 An Integrated Approach

It is clear that our current understanding and measurement of cognition would not have been possible without controlled, captive studies. Yet despite advances in the study of the natural world and the technology that facilitates data collection in the field, the study of animal cognition remains largely biased towards captive settings. Measuring cognition in the wild, however, has the advantage of quantifying the social and ecological determinants of variation in cognition while minimising the adverse effects of captive testing, such as the stress responses caused by isolation or enclosure (Cauchoix et al., 2017; Pritchard et al., 2016). Evaluating cognitive variation in some species may only be possible in captivity, particularly in the case of large primates which are difficult to test. However, adapting the rearing and testing environment to include stimuli that animals would experience in their natural habitat, when measuring ecologically relevant abilities, should be common practice, particularly because test results are often generalised to an entire species (Boogert et al., 2018). At the same time, captivity can buffer some of the shortcomings that make studies in the wild challenging, for instance a small number of trials (Laidre, 2008) and/or individuals (e.g. Isden et al., 2013; Thornton & Samson, 2012). One possible solution may be to test individuals from captive and wild populations with the same tasks to evaluate differences in their performance. For instance, studies with spotted hyenas in wild and captive settings have reported behavioural and performance differences when tested with the same problem-solving apparatus, including differences in the time taken to approach the novel stimulus and the rate of success (Benson-Amram et al., 2013). Likewise, research on animals of the same species has found differences between captive and wild individuals in tool use (Chevalier-Skolnikoff & Liska, 1993), responses to novelty (Forss et al., 2015) and reversal learning (Cauchoix et al., 2017). Studies in wild and captive settings should work to complement each other: research in captivity could help to assess experimentally what conditions affect the development of cognitive abilities in animals, while studies in the wild could evaluate how differences in cognition can influence fitness.

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Appendix S1

Supporting Information For Chapter 3

Table S1.1 Ethogram of chacma baboon behaviours. Shown are all the behaviours recorded in the focal follows carried out during the 2015 and 2016 field seasons. Below is a description of each behaviour classified as either: general activities; aggressive behaviours; submissive behaviours; affiliative behaviours; and self-directed behaviours

	Behaviour
General Activities	**1. Travel:** An individual moves from one location to another.
	2. Travel Foraging: An individual forages whilst moving from one location to another.
	3. Resting: An individual ceases moving from one location to another and instead sits or lies down.
	4. Drinking: An individual bends its body and drinks from a body of water.
	5. Foraging: An individual searches for a food item which it then consumes.
Aggressive Behaviours	**1. Displacement (Active):** A retreat/approach interaction in which an individual moves or causes a conspecific to move away from a resource.

	2. Displacement (Passive): A retreat/approach interaction in which an individual moves or unintentionally causes a conspecific to move away from a resource.
	3. Displacement (Delayed): A retreat/approach interaction in which an individual moves or causes a conspecific to move away from a resource after a small delay from the recipient.
	4. Supplant (Active): A retreat/approach interaction in which an individual intentionally leaves or takes over a resource (food, shade or grooming partner).
	6. Supplant (Delayed): A retreat/approach interaction in which an individual intentionally leaves or takes over a resource (food, shade or grooming partner) after a small delay from the recipient.
	7. Attack: An individual bites, pushes, fights or pulls another intentionally.
	8. Threat: An individual hits (in a sweeping motion) the ground repeatedly and towards the recipient.
	9. Chase: One or several individuals (in support) run after the recipient.
	10. Chase up a tree: One or several individuals (in support) run after the recipient forcing it to climb a tree.
	11. Held up in a trees: One or several individuals (in support) corner the recipient up in a trees, while awaiting at the bottom and in occasion shaking the tree or branch.
	12. Redirection: The recipient of an aggression has an aggressive behavior against an uninvolved third-party.
	13. Coalissionary support: An individual gives support to another (either aggressor or recipient) involved in an aggressive event.

Submissive Behaviours	**1. Avoids:** Individual retreats slowly or quickly when dominant looks, approaches or directs a behavior towards him.
	2. Diverts gaze: Individual looks down or towards another individual.
	3. Scream: High pitch vocalization.
Affiliative Behaviours	**1. Grooming:** The individual spreads the hair of another, pulling out with its hands or mouth.
	2. Genital grooming: The individual spreads the hair of another, pulling out with its hands or mouth around the genital area**.**
	3. Grooming request: Any position that is exposed and relaxed, usually followed by grooming.
	4. Contact: Any specific contact between individuals; for example, back to back.
	5. Hug: An individual surrounds another with its arm(s).
	6. Proximity: An individual is in the immediate surrounding area as another.
	7. Cuddle: Intense contact were an individual leans its upper body against another.
	8. Kiss: Places mouth, slightly open against another's mouth.
	9. Sniff mouth: An individual sniffs the mouth of another.
	10. Touch: An individual briefly touches another's posterior.
	11: Present: In individual presents its hindquarter to another.
	12. Mount: An individual places his feet behind the knee joint of another whilst grabbing their hindquarter.
	13. Lipsmacking: An individual quickly opens and closes its mouth, causing the lips to smack together and the teeth to chatter, making noise.

Self-Directed Behaviours	**1. Self-Scratching:** An individual scratches itself repeatedly and with short fast movements.
	2. Self-Grooming: An individual grooms itself.
	3. Self-touching: An individual will touch itself very quickly.
	4. Genital manipulation: An individual will touch its genitals repeatedly.
	5. Masturbation: A male will masturbate itself. Usually also eats its own ejaculation.
	6. Yawn: An individual (usually male) will yawn in the presence of higher ranking individuals. Usually followed by another self-directed behaviour.

Appendix S2

Supporting Information For Chapter 4

Table S2.1 Spearman rank correlation coefficients, *S*, of the predictor variables used in the statistical analysis of an operant conditioning assessment using coloured corn kernels (N =38) Shown are the correlations coefficients of the predictor variables used in the statistical analysis. Sample size is N=38 individuals in all cases. Individual vigilance and total time were calculated as the median across all trials (1-5). First choice refers to the first choice between each pile of corn in the first trial (Palatable: R; Unpalatable: W).

	Sex	**Age**	**Rank**	**Boldness**	**Vigilance**	**Troop**	**Fst.Ch**	**Total Time**
Sex	1.00							
Age	0.54	1.00						
Rank	0.59	-0.01	1.00					
Boldness	0.12	0.50	-0.20	1.00				
Vigilance	0.19	-0.32	0.49	-0.18	1.00			
Troop	0.01	0.04	0.08	0.15	-0.06	1.00		
First Choice	0.38	0.20	0.16	0.11	0.08	0.09	1.00	
Total Time	0.14	-0.41	0.49	-0.09	0.63	-0.16	0.09	1.00

Appendix S3

Supporting Information For Chapter 5

Table S3.1 Spearman rank correlation coefficients, *S*, of the predictor variables used in the analyses evaluating extractive foraging task involving coloured paper bags. (A) Shown are the correlations coefficients of the variables used in the statistical analysis evaluating first choice of bag (Vig.Ra = median vigilance rate; Ex.Ra = median exploratory rate). N = 84 observations in all cases except for vigilance, where N = 84; (B) Shown are the correlations coefficients of the variables used in the statistical analysis evaluating first bag to be opened and exploratory rate of the correct bag (Vig.Ra = median vigilance rate; Ex.Ra = median exploratory rate). N = 87 individuals in all cases.

(A) Extractive Foraging, First Choice

	Sex	**Age**	**Rank**	**Bold**	**Vig.Ra**	**Exp.Ra**	**Troop**
Sex	1.00						
Age	0.65	1.00					
Rank	0.54	0.13	1.00				
Boldness	0.16	0.45	-0.16	1.00			
Vigilance Rate	0.21	0.31	0.09	-0.11	1.00		
Exploratory Rate	0.32	0.25	-0.21	0.13	-0.12	1.00	
Troop	-0.05	-0.12	0.15	-0.05	-0.01	0.03	1.00

(B) Extractive Foraging, First Bag to Open; Exploration of the Correct Bag

	Sex	**Age**	**Rank**	**Bold**	**Exp.T**	**Vig.Ra**	**Troop**
Sex	1.00						
Age	0.65	1.00					
Rank	0.54	0.13	1.00				
Boldness	0.16	0.45	-0.16	1.00			
Exploratory Time	-0.12	0.02	0.07	-0.02	1.00		
Vigilance Rate	0.06	0.20	0.14	-0.05	0.41	1.00	
Troop	-0.05	-0.12	0.15	-0.05	-0.14	-0.17	

Appendix S4

Supporting Information For Chapter 7

Patch protocol

During the focal follows (refer to Chapter 3 for more details), information regarding patch occupation was collected. Baboons at Tsaobis forage on two distinct habitats: riparian woodland and hills (Cowlishaw & Davies, 1997). Each habitat is defined by a number of food patches that consist of tree, herb or bush species, which serve as the main food source of the baboons. In the focal follows, a patch was considered as any of the species listed in Table S4.1. In the case of trees, a patch could consist of a single tree, or include several trees if the canopy of a tree of the same or different species overlapped with another the focal individual could forage from. In the case of herbs and shrubs, a patch could consist of a single plant, or several if another herb/shrub of the same species was within a 5 m. radius from the original one the focal individual was feeding from (for a similar patch protocol see: Marshall et al., 2012). Patch occupation was determined as *unoccupied* if the focal individual foraged from a patch where no other conspecific, either inside the patch or within 2m was actively foraging. Likewise, patches were considered *unoccupied* if there were conspecifics foraging from or within 2 m from it but engaged in an activity that was not foraging (i.e. resting, grooming). A patch was considered *occupied* if the focal individual entered a patch where other conspecifics were actively foraging from it.

Table S4.1 List of main plants considered for patch information. Shown are the tree, herb and shrub species (in *italics*) recorded during focal follows

	Species
Trees	*Faidherbia albida*
	Prosopis glandulosa
	Tapinanthus oleifolius
	Acacia tortilis
	Acacia erioloba
	Ficus sycomorus
Herb/Shrubs	*Salvadora persica*
	Monechma cleomoides
	Nicotiana glauca
	Sesamum capense
	Commiphora virgata

Table S4.2 Spearman rank correlation coefficients, *S*, of the predictor variables used in the analyses evaluating participation in an extractive foraging task involving coloured paper bags. Shown are the correlations, between the predictor variables in the statistical analysis. (A): N = 104 for activity/111 for the rest; (B): N = 111 observations in all cases in the associative learning task; and (C): N = 111 observations in all cases in the associative learning task.

(A) H1, Extractive Foraging Task

	Activity	**Sex**	**Age**	**Rank**	**Boldness**
Activity	1.00				
Sex	-0.17	1.00			
Age	-0.12	0.57	1.00		
Social Rank	-0.07	0.58	0.03	1.00	
Boldness	-0.08	0.10	0.51	-0.22	1.00

(B) H2, Extractive Foraging Task

	Scrounge	Sex	Age	Rank	Boldness
Scrounge	1.00				
Sex	-0.04	1.00			
Age	-0.15	0.57	1.00		
Social Rank	0.24	0.58	0.03	1.00	
Boldness	-0.27	0.10	0.51	-0.22	1.00

(C) H4, Extractive Foraging Task

	Sex	Age	Rank	Boldness
Sex	1.00			
Age	0.57	1.00		
Social Rank	0.58	0.03	1.00	
Boldness	0.10	0.51	-0.22	1.00

Table S4.3 Spearman rank correlation coefficients, *S*, of the predictor variables used in the analysis evaluating participation in a second-order conditioning task. Shown are the correlations between the predictor variables in the statistical analyses. (A): N = 156 for activity/162 for the rest; (B): N = 162 observations in all cases; (C): N = 162 observations in all cases; and (D): N = 162 observations in all cases in the SOC task.

(A) H1, Second-Order Conditioning Task

	Activity	**Sex**	**Age**	**Rank**	**Boldness**
Activity	1.00				
Sex	-0.03	1.00			
Age	-0.02	0.64	1.00		
Social Rank	-0.04	0.73	0.27	1.00	
Boldness	0.11	0.12	0.36	0.11	1.00

(B) H2, Second-Order Conditioning Task

	Scrounge	**Sex**	**Age**	**Rank**	**Boldness**
Scrounge	1.00				
Sex	0.05	1.00			
Age	0.19	0.64	1.00		
Social Rank	-0.15	0.73	0.27	1.00	
Boldness	-0.09	0.12	0.36	0.11	1.00

(C) H3, Second-Order Conditioning Task

	Active.Agg	**Passive.Agg**	**Self-scratch**	**Self-groom**	**Focal-trial interval**
Active.Agg	1.00				
Passive.Agg	0.16	1.00			
Self-scratch	0.19	0.16	1.00		
Self-groom	0.07	0.08	0.32	1.00	
Focal-trial interval	-0.03	-0.08	-0.04	-0.05	1.00

(D) H4, Second-Order Conditioning Task

	Sex	**Age**	**Rank**	**Boldness**
Sex	1.00			
Age	0.64	1.00		
Social Rank	0.73	0.27	1.00	
Boldness	0.12	0.36	0.11	1.00

Appendix S5

Supplementary Information For Chapter 8

Table S5.1 Spearman rank correlation coefficients, *S*, of the predictor variables used in the analyses evaluating feeding techniques in an associative learning task involving coloured kernels and a second-order conditioning task. Shown are the correlations between the predictor variables in the statistical analyses. (A): N = 162 total observations in the mechanical behaviours in associative learning task involving coloured kernels; (B): N = 81 total observations in in the physical position in the SOC task. Tables show *S* and its corresponding N. Variables with a Spearman correlation coefficient >0.70, were not used in the same model.

(A) Associative Learning Task I

	Time feeding	Age	Rank	Agg. Within	Agg. Previous
Total time feeding	1/147				
Age	-0.29/ 147	1/162			
Social Rank	0.32/ 147	-0.08/ 162	1/ 162		
Aggression within trial	-0.56/ 146	0.24/ 161	-0.17/ 161	1/ 161	
Aggression in previous trial	-0.10/ 115	0.22/ 123	-0.19/ 123	0.09/ 123	1/ 123

(B) Associative Learning Task 2

	Time feeding	Age	Rank	Agg. Within	Agg. Previous
Total time feeding	1/ 80				
Age	0.06/ 80	1/ 81			
Social Rank	0.40/ 80	0.27/ 81	1/ 81		
Aggression within a trial	-0.31/ 80	-0.11/ 81	0.08/ 81	1/ 81	
Aggression in previous trial	-0.02/ 53	-0.19/ 54	0.11/ 54	0.20/ 54	1/ 54