INNOVATION AND PROBLEM SOLVING IN BAT EARED FOXES, *OTOCYON MEGALOTIS*

By

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DECLARATION

I, Paul Juan Jacobs, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree. I furthermore cede copyright of the dissertation in favour of the University of the Free State.

Signature………………………………………………………….

Date…………………………………………………………………..

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TABLE OF CONTENTS

Chapter 1: Literature review

Chapter 2: First report of a myrmecophageous bat-eared fox *Otocyon megalotis* hunting a hare *Lepus sp*.

Chapter 3: Exploration diversity, persistence, neophobia and their influence on problem solving in bat-eared foxes, *Otocyon megalotis*

Chapter 4: Research synthesis and conclusions

ABSTRACT

Cognition, defined as the acquisition, processing, storage and use of information, can have direct fitness consequences, and has emerged as an important subfield within behavioural ecology. Individual differences in cognitive performance have been correlated, *inter alia*, with relative brain size, the complexity of a species' social and ecological environment, and personality. Personality refers to stable, long-term behavioural, emotional, and physiological differences in suites of traits among individuals within a species. In order to observe differences in cognitive performance within a species, rates of innovation and problem solving tasks are typically used. Innovation can be operationally defined as 'a new or modified learned behaviour not previously found in the population'. Problem solving includes decision making allowing animals to overcome obstacles to reach a goal. To date, the majority of studies investigating innovation and problem solving did so by presenting novel problems to isolated captive animals, whose responses may not reflect those seen in natural and social contexts. Moreover, field experiments have primarily been restricted to birds and primates. Tests under natural circumstances are important as they are ecologically and biologically relevant. For example, wild individuals may have divided attention as they need to be vigilant in the presence of predators, compared to captive individuals, for whom predators are not a consideration. The aim of this study was to investigate individual differences in innovation and problem solving in bat-eared foxes (*Otocyon megalotis*) through observation and an object manipulation task Observations offered an opportunity to witness innovations in the wild. I observed a specific

novel foraging event from a female bat-eared fox. This innovation event included the hunting and killing of a hare (*Lepus sp.*) in order to consume this large prey animal, which was unusual, considering the preferred invertebrate diet of bat-eared foxes, and their dentition specialized for smaller prey. The object manipulation task included manipulating part of a contraption in order to solve a problem and used to determine the influences of personality on learning and problem solving. Foxes were proficient learners in the object manipulation task, where persistence and exploration diversity were important aspects of problem solving. Persistence and exploration behaviour were correlated in the problem solving of bat-eared foxes, providing support for the basis that more explorative and more persistent individuals may be more flexible in solving problems. The effects of high neophobia was only revealed when all trials were considered instead of only the initial trial, thus a higher neophobia may have a long term effect on problem solving ability compared to individuals who are only moderately neophobic. Bat-eared foxes have shown proficient learning abilities and rapidly learned when tasks were presented to them. I show that innovation, problem solving, learning, persistence, neophobia and exploration can influence aspects of animal cognition, further extending our knowledge of animal cognition by using a natural population of bat-eared foxes. These correlates are important for the fitness and survival of bat-eared foxes and their offspring, as foxes can rapidly assess foraging situations (such as extracting termites from a termite mound), opportunistically hunt novel prey and learn new foraging techniques, which can all lead to increased foraging success. I discuss potential future research into bat-eared fox cognition, such as investigating persistence in an unsolvable problem solving task. Unsolvable tasks outside of domestic dog research have been few and are highly encouraged to determine the influence of persistence

on problem solving performance. Alternative contexts for the measurement of personality (exploration-avoidance) are also discussed, for example, using an open-field test, which includes monitoring an individual explore a novel space or a known space with novel objects/stimuli in it.

Keywords: bat-eared fox, cognitive ecology, innovation, personality, problem solving

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1
LITERATURE REVIEW

1.1. General introduction

In the past decade, cognitive ecology has emerged as an important field within behavioural ecology. Cognition, broadly defined, is the acquisition, processing, storage and use of information (Griffin, Guillette, & Healy, 2015). Cognition encompasses a large variety of abilities such as perception, learning, memory, and decision-making (Dukas, 2004; Griffin et al., 2015; Shettleworth, 2001). Typical research focuses on how the effects of information processing and decision-making impacts animal fitness in their social and ecological environment (Dukas, 1998; Healy & Braithwaite, 2000; Hutchins, 2010; Real, 1993; Shettleworth, 2001): in a complex, variable environment, the ability to rapidly learn new survival techniques can confer a fitness advantage to the learner (Dukas, 2004). Learning can be defined as the ability to acquire a neuronal representation of either a new association between a stimulus and an environmental state, or a new association between a stimulus and behavioural pattern (Dickinson, 2010, 2012; Dukas, 2002; Pearce, 2013; Pearce & Bouton, 2001) Learning has been demonstrated in a variety of species ranging from vertebrates (MacPhail, 1982; Macphail & Barlow, 1985), to invertebrates (Dukas, 2007), to species, such as *Escherichia coli*, that lack neural tissue (Tagkopoulos, Liu, & Tavazoie, 2008). Learning is a trait of general intelligence assumed to be linked to overall brain size (Roth & Dicke, 2005), with the learning capability of vertebrates to increase with brain size (Rensch, 1956).

1.2. Larger brains size, brain regions and cognitive complexity

1.2.1. Larger brain size and brain regions

Brain tissue is energetically expensive to grow and maintain (Aiello & Wheeler, 1995). In addition to the energetic costs associated with higher metabolic rates, larger brains take longer than smaller brains to reach structural, functional and behavioural maturity, even after reaching full volume (Barrickman, Bastian, Isler, & van Schaik, 2008; Schoenemann, Budinger, Sarich, & Wang, 2000). It is therefore highly unlikely that larger brains evolved without conferring a significant, direct benefit to the individuals with increased neural tissue (Dunbar, 1998; Dunbar & Shultz, 2007). General intelligence has been assumed to be linked to overall brain size (Roth & Dicke, 2005). However, monkeys possess brains that are much smaller than those of ungulates, but monkeys' higher cognitive and behavioural flexibility seems clear (Gibson, Rumbaugh, & Beran, 2001; Marino, 2002; Reader & Laland, 2002; Roth & Dicke, 2005). Thus, there does not appear to be a clear, overt link between absolute brain size and cognitive performance. Contemporary studies of brain evolution tend to focus on the size of particular areas of the brain, such as the neocortex, on the assumption that a focus on brain areas involved in the trait of interest is appropriate (Deaner, Isler, Burkart, & van Schaik, 2007; Reader & Laland, 2002). Cognitive traits such as innovation (displaying new or modified behaviours to solve novel challenges or familiar problems in a novel way (Ramsey, Bastian, & van Schaik, 2007; Reader & Laland, 2003)) and problem-solving abilities require behavioural flexibility involving a range of processes, and thus appear unlikely to be restricted to a specific brain area (Sol, Bacher, Reader, & Lefebvre, 2008). Specific brain areas however, have been associated to such skills, with the neocortex broadly accepted to underpin most basic and higher cognition (innovation, learning and memory) in mammals (Baars & Gage, 2007; Carlson, 2012; Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010; Reader & Laland, 2002).

1.2.2. Cognitive complexity

Cognitive complexity or complex cognition are terms commonly used in cognitive research, but they have rarely been precisely defined (Barrett, Henzi, & Rendall, 2007; Brown, 2012; Marino, 2002; Marino et al., 2007; Taylor, Elliffe, Hunt, & Gray, 2010). Broadly speaking, complex cognition has been suggested to be: all mental processes that are used by an individual for deriving new information out of given information, with the intention to make decisions, solve problems, and plan actions (Knauff & Wolf, 2010). Cognitive complexity has been linked to both social and ecological processes. For example, among primates, species with cognitively demanding social environments are also better able to solve foraging and other ecological problems (Reader & Laland, 2002). This suggests that social and ecological processes are not necessarily mutually exclusive, as most problems are ultimately of ecological relevance (Shultz & Dunbar, 2007).

The ecological hypothesis includes the "cognitive buffer" and is one of the ideas that link cognitive and ecological complexity. This hypothesis has two primary assumptions: the first, that larger relative brain size allows flexibility in the utilisation of information and the production of behavioural responses to environmental change (Sol, 2009a, 2009b); while the second assumes that individuals can adaptively respond to novel socio-ecological challenges through general cognitive processes such as innovation and learning (Sol, 2009a, 2009b). Birds and mammals that are behaviourally flexible have a higher survival rate when introduced into novel environments due to the benefits of enhanced cognitive performance associated with a larger relative brain size (Sol et al., 2008; Sol, Székely, Liker, & Lefebvre, 2007). The environmental change induced by being introduced into a novel environment may require innovation to increase fitness and/or survival in the form of anti-predatory responses against novel predators (Berger, Swenson, & Persson, 2001), the adoption of new food resources when the traditional ones become scarce (J. A. Estes, Tinker, Williams, & Doak, 1998), or the adjustment of breeding behaviour to the prevailing ecological conditions (Brooke, Davies, & Noble, 1998).

Specific complex ecological processes such as extractive foraging (Dunbar, 1998; S. T. Parker & Gibson, 1977) and dietary requirements (e.g. fruit; Clutton-Brock & Harvey, 1980; Gittleman, 1986)have also been proposed to led to a larger relative brain size. Extractive foraging requires individuals to extract resources from a matrix in which they are embedded (e.g. they must remove fruit pulp from a case, stimulate gum flow from a tree, extract termites from a termitarium, or hunt species that are cryptic or behave evasively; Dunbar, 1998). Extractive foraging is commonly associated with tool making or tool use, as the tools are often used for the extraction of the hard to access food (S. T. Parker & Gibson, 1977). Diet has also been correlated with a larger relative brain size in frugivores (Clutton-Brock & Harvey, 1980; Dunbar, 1998), omnivores and carnivores (Gittleman, 1986). Frugivorous diets are ephemeral and patchy in distribution which requires more memory to find them(Dunbar, 1998). Carnivores require complex foraging strategies involving selection for rapid prey detection, pursuit, capture (especially forepaw manipulation) and consumption (Gittleman, 1986). These complex foraging strategies and extractive foraging have been associated with a larger neocortex in primates (Dunbar, 1998), but only relative brain size without specific brain regions in Carnivores (Gittleman, 1986; Pérez-Barbería, Shultz, & Dunbar, 2007). Moreover, only the relative size of the whole brain was compared for mammals that were introduced into novel environments, with the general trend that individuals that had a larger relative whole brain survived better when introduced into novel environments (Sol et al., 2008). This could imply several brain regions at work however; general consensus thus far suggests that the neocortex is important as these ecological factors were positively associated with the neocortex in primates (Dunbar, 1998).

Social processes have also been argued to contribute to a larger relative brain size. This idea is encapsulated in the social complexity hypothesis, which includes the "Machiavellian intelligence" and "social brain" hypotheses (Dunbar, 1998; Dunbar & Shultz, 2007; Whiten & Byrne, 1988). The Machiavellian intelligence hypothesis focuses on characteristics of mindreading, manipulation, and deception for social complexity (Whiten & Byrne, 1988). The development of these skills will allow an individual to exploit other individuals within a group for its own benefit, but in turn could likely create an arms race as other individuals will develop social skills to avoid being manipulated or deceived. This hypothesis also suffers from a lack of quantitative empirical evidence as supporting evidence was anecdotal at best (Dunbar, 1998). The social intelligence hypothesis argues that large brains are necessary for dealing with the complexities of social life (Dunbar & Shultz, 2007; Jolly, 1966; Pérez-Barbería et al., 2007; van Schaik, Isler, & Burkart, 2012). For example, individuals with larger brain regions, such as the neocortex, should be able to keep track of more individual relationships and able to respond appropriately during interactions with other individuals (Barton, 1996; Deaner et al., 2007; Dunbar, 1992; Shultz & Dunbar, 2007). Social structure has been found to be a relevant factor in relative neocortical volume in primates (Barton, 1996), bats (Barton & Dunbar, 1997), carnivores (Dunbar & Bever, 1998; Finarelli & Flynn, 2009; Gittleman, 1986), ungulates (Pérez-Barbería & Gordon, 2005) and odontocete cetaceans (Marino, 1996).

1.3. Cognition

1.3.1 Operant conditioning and memory

Operant conditioning is considered to be one of the most basic forms of cognition, consisting of the formation of simple stimulus-response associations (Kirsch, Lynn, Vigorito, & Miller, 2004; Pearce & Bouton, 2001). In contrast to classical conditioning – where unconditioned autonomic responses become associated with a novel stimulus (Dickinson, 2010;

Kirsch et al., 2004; Pearce, 2013; Pearce & Bouton, 2001)- operant conditioning is a change in behaviour through the use of reinforcement given after a desired response (Skinner, 1938). In light of the proposed Law of Effect (Thorndike, 1911), trial-and-error or accidentally-occurring behaviour in a goal directed action could be reinforced if the behaviour was rewarded (or: positively reinforced). The reinforced behavioural pattern is more likely to reappear with subsequent presentations of the same problem (Pearce, 2013), where individuals learn to associate said behavioural pattern with a specific problem, commonly referred to as associative learning (Thorndike, 1898). An example of a reinforced behavioural response to a problem comes from rats running down an ally or maze (Pearce, 2013). For example, Elliot (1929) trained rats to navigate a maze for a specific food reward, but when the expected food reward quality was reduced, rats started to incur more errors compared to the control group. The change in the expected reward caused more errors, suggesting that individuals were able to expect certain outcomes for specific actions, but when these expected outcomes changed, individuals did not associate the previous behavioural pattern with the reward. This has led to the expectancy theory of operant conditioning, which gained further support in a reinforce devaluation design (Adams & Dickinson, 1981). An example of the reinforce devaluation design includes rats that were trained on two stimuli (food pellets and sucrose solution), but after a number of sessions, one stimulus was associated with a mild poison (Adams & Dickinson, 1981). The association of one of the stimuli to the mild poison was so effective that individuals completely rejected the stimulus associated with the poison (Adams & Dickinson, 1981).

Learning to anticipate future events or expecting specific outcomes on the basis of past experiences with the consequences of one’s own behaviour is a simple form of learning that humans share with most other animals, including invertebrates (Brembs, 2003). Thorndike (1911) even argued that despite the range of potential problems an animal can confront, the majority of problems are solved in the same manner (operant conditioning). The biological relevance of operant conditioning allows animals to learn about the consequences of their actions which have far reaching implications, as individuals can associate aspects of their ecological environment with potential increases and/or decreases in fitness and survival.

Memory consists of implicit and explicit memory, where implicit memory involves the unintentional, non-conscious form of retention that can be contrasted with explicit memory, which involves conscious recollection of previous experiences (Baars & Gage, 2007; Schacter, 1992). Moreover, explicit memory includes semantic memory and episodic memory, where semantic memories include general world knowledge and episodic memory storage and recollection of life-events (Baars & Gage, 2007). For example, semantic memory would include knowing that the capital of France is Paris, where episodic memory would include a memory of visiting Paris (Baars & Gage, 2007). Episodic memory is associated with the hippocampus brain region whereas semantic memories are associated with the neocortex (Baars & Gage, 2007; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006). Both implicit and explicit memory are important in short term and long term memory, with short term and long term memory operating in the neocortex (Baars & Gage, 2007). Conditioned learning is part of the implicit memory system (Baars & Gage, 2007), which suggests that individuals recall what they have learned through conditioning unconsciously.

1.3.2. Innovation

The capacity to innovate (displaying new or modified behaviours to solve novel challenges or familiar problems in a novel way (Ramsey et al., 2007; Reader & Laland, 2003)) has been shown to enhance an innovator’s access to food (Laland & Reader, 1999; Overington, Cauchard, Côté, & Lefebvre, 2011), mates (Keagy, Savard, & Borgia, 2011), and even improve the fitness of their offspring (le Roux et al., 2013). Innovation may have vast evolutionary significance as it may allow animals to utilise new habitats, exploit novel resources, and cope with environmental change (Bókony et al., 2014; Griffin & Guez, 2014; Ramsey et al., 2007; Reader & Laland, 2003).

1.3.3. Necessity and capacity: drivers of innovation

Innovative behaviour has been described in a wide range of taxa, and several hypotheses have been proposed to explain the occurrence of innovation in wild animals. These hypotheses include unpredictability and predictability (Kummer & Goodall, 1985; Lee & Moura, 2015), necessity (Bókony et al., 2014; Griffin & Guez, 2014; Reader, 2003; Reader & Laland, 2003) and capacity (Bókony et al., 2014; Reader & Laland, 2003). These hypotheses implicate the importance of external factors (social and/or ecological environment) that drive innovation. The first hypothesis (Kummer & Goodall, 1985; Lee & Moura, 2015) proposes that individuals are likely to innovate if, for example, resource conditions and their variation cannot be predicted (Lee & Moura, 2015). An example of this includes New Caledonian crows (*Corvus* *moneduloides*) that have a low biomass of invertebrate prey that is not concealed, but an abundant biomass of concealed prey, which can be extracted using tools (Lee & Moura, 2015; Rutz & St Clair, 2012). This led to the exploitation of a woodpecker-like niche on the island, with the use of tools to extract concealed prey (Rutz & St Clair, 2012). The second include predictability or stability, and is likely to appear during periods of excess in leisure and energy (Kummer & Goodall, 1985; Reader & Laland, 2001). This is generally exemplified by captive conditions, for example, a captive dingo (*Canis lupus dingo*) moved a table to reach a previously out of reach food item (Smith, Appleby, & Litchfield, 2012).

The "necessity drives innovation" hypothesis proposes that innovation will occur during time of necessity (Bókony et al., 2014; Griffin & Guez, 2014; Lee & Moura, 2015; Reader, 2003; Reader & Laland, 2003). Energetically challenging habitats (food shortage and dry seasons; (Lee & Moura, 2015; Reader & Laland, 2001) and competition in prevailing ways of resource acquisition (Bókony et al., 2014; Griffin & Guez, 2014; Reader, 2003; Reader & Laland, 2003) allow necessity to arrive. An example of food shortage driving innovation are capuchin monkeys (*Cebus sp.*), that during a time of low availability of fruit resources and key tree foods started to extract termites from their nests suggesting a strong need to obtain energy or nutrients (Lee & Moura, 2015). An example for competition driving innovation are guppies (*Poecilia reticulata*) that were rated on innovative tendency based on size and food deprivation, with smaller sized and food deprived fish more likely to innovate compared to larger and non-food deprived fish (Laland & Reader, 1999). The necessity hypothesis has considerable empirical support from work with fish (Laland & Reader, 1999), birds (Cole, Morand-Ferron, Hinks, & Quinn, 2012; Morand-Ferron, Cole, Rawles, & Quinn, 2011) and primates (Kendal, Coe, & Laland, 2005;

Reader & Laland, 2001), in which juveniles and low-ranking subordinates tend to show high innovative tendencies. However, conflicting results have been observed (Boogert, Reader, & Laland, 2006; Bouchard, Goodyer, & Lefebvre, 2007); for example, Boogert et al. (2006) found that high-ranking starling (*Sturnus vulgaris*) individuals innovated more than low-ranking ones.

A third prominent hypothesis – the "cognitive capacity" hypothesis (Bókony et al., 2014; Reader & Laland, 2003)– proposes that innovative abilities may be determined by cognitive skills, such as the capacity for learning and reasoning (Hauser, 2003). This hypothesis implicates an animal's relative brain size as the primary drivers of innovative behaviour, as the ability to learn, and reason requires a larger relative brain size (Reader & Laland, 2002). A link between brain size and innovation has received empirical support, with the largest number of field reports of innovation coming from large-brained avian and primate species, compared to their smaller-brained counterparts (Lefebvre, Reader, & Sol, 2004).

These hypotheses of unpredictability, predictability, necessity and capacity are not mutually exclusive, and each predicts that individuals may differ consistently in their propensity to innovate, be it due to the social and ecological environment or the capacity to innovate (Bókony et al., 2014). The social and ecological environment and the capacity to innovate are closely linked, as a complex ecological and social environment has been proposed as the driver for the evolution of larger relative brain size, allowing for the capacity to innovate or to perform complex cognition (Bókony et al., 2014).

1.4. Individual, sexual, ontogenetic and morphological differences

Mounting evidence suggests that cognitive traits are not fixed for each species, but that personality can be linked to variation in cognitive performance (Griffin et al., 2015; Rowe & Healy, 2014). “Personality” or “temperament” refers to stable, long-term behavioural, emotional, and physiological differences in suites of traits among individuals of the same species (Carere & Locurto, 2011; Gosling, 2001; Kurvers et al., 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004; Webster & Lefebvre, 2001). Personality can be divided into five trait categories. The first three relate to the ecological domain: 1) shyness-boldness, which is the reaction to risky situations but not novel situations, 2) exploration-avoidance, which is an individuals’ reaction to novel stimuli (e.g. food, habitat and objects), and 3) activity, which is general level of activity of an individual (Réale et al., 2007). The next two personality categories are expressed in a social context, i.e., 4) aggressiveness: an individual’s reaction to agonistic encounters with conspecifics, and lastly 5) sociability, an individual’s reaction to the presence or absence to conspecifics (which excludes aggressive behaviour; Réale et al., 2007). Within these personality category traits, individuals have a specific personality type (Griffin et al., 2015; Réale et al., 2007; Sih et al., 2004). For example, neophobia (Benson-Amram & Holekamp, 2012; Biondi, Bó, & Vassallo, 2010; Cole, Cram, & Quinn, 2011; Webster & Lefebvre, 2001) and exploratory tendency (Benson-Amram & Holekamp, 2012; Biondi et al., 2010; Cole et al., 2011; Webster & Lefebvre, 2001) fall within the exploration-avoidance personality category. Exploration is the degree to which an individual investigates a novel area or object (Benson-Amram & Holekamp 2012; Cole et al. 2011; Biondi, Bó, & Vassallo, 2010), whereas neophobia is the avoidance of novel stimuli (Benson-Amram & Holekamp, 2012; Bergman & Kitchen, 2009). “Persistence” has not been included as a personality type within the personality trait categories by Réale et al. (2007), but may be associated as a personality type of measurement, as individuals vary within this trait (Benson-Amram & Holekamp, 2012; Griffin & Diquelou, 2015; Thornton & Samson, 2012). Persistence is a motivational measure of task-directed engagement, linked to variety of parameters such as feeding motivation and ecological relevance of the task for the species being tested (reviewed by Griffin and Guez (2014).

Several studies have found contradicting results between the correlation of personality types and cognitive performance (Biondi et al., 2010; Cole et al., 2011; Guillette, Reddon, Hurd, & Sturdy, 2009; Hopper et al., 2014; Sneddon, 2003). For example, problem solving was inhibited by neophobia in spotted hyenas(Benson-Amram & Holekamp, 2012), whereas Cole et al. (2011) found no influence of neophobia and exploration behaviour on a lever and string pulling task in great tits (*Parus major*). Due to conflicting results as to how personality interacts with cognitive performance (Carere, 2003; Cole et al., 2011; Guillette et al., 2009; Sneddon, 2003), the relationship between cognitive performance and personality remains unclear and still constitute an open topic of investigation (Cole et al., 2011; Hopper et al., 2014).

Cognitive performance may also vary between sexes, along an ontogenetic gradient, and morphology (Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014). Primate females are more likely to innovate than males (Box, 1991, 1997; Kawai, 1965; Kummer & Goodall, 1985). For example, Box (1991, 1997) provided examples of increased investigation by females, noting that females of some primate species appear more adaptively responsive to environmental change compare to males. Birds have shown no correlation of sex to problem solving (Biondi et al., 2010; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole et al., 2011), with a few exceptions (Range, Bugnyar, Schlögl, & Kotrschal, 2006; Titulaer, van Oers, & Naguib, 2012). For example, Range et al. (2006) determined that male ravens (*Corvus corax*) were significantly better in the acquisition of an object manipulation task compared to females. Titualer, van Oers and Naguib (2012) found that fast-exploring great tit males showed more flexible learning abilities compared to slow-exploring males, and that females operated in the opposite direction, with female slow-explorers outperforming fast explorers. Developmentally, juveniles of all species are generally more curious and explorative than adults, but may not exhibit enhanced cognitive performance (Kendal et al., 2005; Kummer & Goodall, 1985), a finding supported by studies demonstrating that juvenile spotted hyenas, meerkats (*Suricata suricatta*) and chimango caracara (*Milvago chimango*) were less neophobic and more explorative compared to adults (Benson-Amram & Holekamp, 2012; Biondi et al., 2010; Thornton & Samson, 2012). Benson-Amram and Holekamp (2012) speculated that juvenile spotted hyenas may have more protection and free time than adults to devote to exploration and problem solving, and that despite being more explorative and less neophobic, may not have the required ability to solve some puzzles due to physical ability. Hopper et al. (2014) and Reader and Laland (2001) found no effect of age on chimpanzee (*Pan troglodytes*) problem solving success or increased innovative tendencies. Lastly, no evidence to date has shown that any state-based measure of motivation, such as body condition or body fat index, correlates with problem-solving performance (Aplin, Sheldon, & Morand-Ferron, 2013; Bókony et al., 2014; Cole et al., 2011; Morand-Ferron et al., 2011; Overington et al., 2011).

1.5. Canine cognition

Members of the family Canidae have been used in a number of cognitive tests, although the bulk of research has focused on the domestic dog (*Canis familiaris*) (reviewed by Bensky, Gosling, and Sinn (2013)). Domestic dogs have been a model species for the study of cognition because of their domestication history and accessibility. Research on dog cognition is being done in a wide variety of scientific disciplines, including ethology, evolutionary anthropology, behavioural analytics, developmental psychology, and neuroscience (Bensky et al., 2013). Several other social and non-social cognitive tests have been performed on dogs, with social cognition investigating responses to human cues, perspective taking, dog-human communication and social learning, whereas non-social cognition investigated how dogs perceive physical stimuli that make up their environment, how they develop mental representations of these stimuli, and/or how dogs utilize abiotic elements to solve a variety of tasks (Bensky et al., 2013). The primary focus of canine cognition currently has investigated similarities and differences between dogs and wolves (*Canis lupus*) to answer questions regarding the influence of domestication on dogs' social and individual learning (Frank & Frank, 1985; Frank, Frank, Hasselbach, & Littleton, 1989; Gácsi et al., 2009; Hare & Tomasello, 2005; Range, Möslinger, & Virányi, 2012; Udell, Dorey, & Wynne, 2008; Virányi et al., 2008). Present findings suggest that dogs are better at interpreting human social cues, such as pointing to hidden food, compared to wolves (Hare, Brown, Williamson, & Tomasello, 2002; Miklósi et al., 2003). Dogs ask for help from humans, resorting to gaze at humans if a task was impossible to solve, whereas wolves continue to try and solve the task by themselves (Miklósi et al., 2003).

Despite this, studies comparing wolves and dogs on simple non-social problem solving or memory tasks typically find that wolves perform as well, if not better than dogs (Frank, 1980; Frank & Frank, 1982; Frank et al., 1989). A few cases of higher cognition have been documented, such as M-E understanding in dogs in a support task (Range, Hentrup, & Virányi, 2011) and the basic understanding of connectivity (Riemer, Müller, Range, & Huber, 2014). A support problem is a problem-solving task where a reward (food) is out of the subjects' reach, but the reward is resting on a support structure that is within the subject's reach (Range et al., 2011). Innovation has rarely been observed in canids. However, an observation by Smith et al. (2012) indicated that a dingo moved a table to reach a previously out of reach food item. Tasks regarding individual differences in canids are lacking (Bensky et al., 2013), with few studies contributing or questioning the contribution of individual differences to cognitive performance (Aust, Range, Steurer, & Huber, 2008; Leonardi, Vick, & Dufour, 2012; Nippak et al., 2003).

1.6 Bat-eared foxes

Bat-eared foxes (*Otocyon megalotis*) have one of the smallest brains in the canid family, with the mean encephalisation quotient of 1.10 compared to a mean of 1.41 of 60 canid species studied (Boddy et al., 2012). Despite this small brain size, they have exhibited behaviour that suggests promising cognitive abilities. In the social domain, bat-eared foxes exhibit a fairly simple structure. Small family groups forage together, with monogamous pair bonds said to last for years (Lamprecht, 1979; Malcolm, 1986). This pair bond is important as males guard pups at the den while the female forages, directly influencing reproductive success (Wright, 2006). Pups stay with the parents for 5-6 months before dispersing (Clark, 2005). Bat eared foxes have a similar core social structure to other fox-like canids, that is, the mated pair; however, bat-eared foxes are considered the most socially tolerant among them, due to an increased frequency of occurrence of social behaviours, such as allogrooming, playing and sleeping/resting in contact (Kleiman, 1967; Lamprecht, 1979). They are not highly territorial, with general interactions between groups described as amicable or neutral. It is not uncommon for different foxes from different social groups to forage independently in the same area (Koop & Velimirov, 1982; Malcolm, 1986; Nel, 1993). Bat-eared foxes are also known for being playful into adulthood (Lamprecht, 1979), which has been proposed to provide experience to generate novel solutions to challenges in a social and physical environment (Bateson, 2014). For example, play may allow individuals to extract social information from games played and by observing third-party interactions (Bradshaw, Pullen, & Rooney, 2015). Moreover, play in juveniles may promote obtaining information about an individuals' physical and social environment, making learning easier (Held & Špinka, 2011).

Anecdotal observations suggests that teaching may occur in this species, with fathers teaching offspring foraging techniques (Nel, 1999). Teaching is complex and in order to prove its existence, three criteria need to be met: 1) an individual, A, changes its behaviour only in the presence of a naïve observer, B 2) A incurs some cost, or obtains no immediate benefit and 3) as a result of A's behaviour, B acquires knowledge or skills quicker than it would otherwise, or that it would not have learned at all (Thornton & Raihani, 2010). The former criteria sets teaching apart from social learning, in which naïve individuals acquire information from other individuals (Thornton & Raihani, 2010). Observations of teaching with these three criteria in mind, have been mostly absent, due to the difficulty of providing evidence for all three criteria, as only three studies have satisfied all three criteria (Thornton & Raihani, 2010). For example, in meerkats, older group members gradually introduce pups to live, mobile prey, with adults incurring costs as live prey might escape, however, pups' handling skills improve as a result of practising with live prey (Thornton & Raihani, 2010).

Bat-eared foxes are also purported to show well-developed cognitive skills related to their complex ecological environment. It has been suggested that foxes use resource mapping of termite mound locations, including knowledge of when these termite mounds are depleted (Lourens & Nel, 1990). This implies that bat-eared foxes should have some degree of proficient memory to recall the location of termite mounds. Bat-eared foxes also exhibit innovative abilities, through the provision of pups with dung that has ensconced insects (le Roux et al., 2013). This is unique as bat-eared foxes were not previously known to provide food to offspring at the den other than milk (Pauw, 2000). Although several of these factors suggest that bat-eared foxes may excel in both social and ecological domains of cognitive ability, no one, to my knowledge, has previously assessed cognitive skills in this species.

1.7. Aim and Objectives

Aim

This study was undertaken to address basic questions about bat-eared fox cognitive performance within the ecological context:

Objectives

1) To conduct observations of natural behaviour in wild bat-eared foxes to determine the possible ecological relevance and prevalence of innovation.
2) To determine how neophobia, exploration and persistence influences learning and problem solving abilities of wild bat-eared foxes.

1.8 Chapters outline

For any study of animal cognition, it is invaluable to provide ecological validation of results, and base any experiments on observations made of natural behaviours. Although the experiments were done by me, I always had help with everything and therefore will use the plural in all cases in this thesis. In Chapter 2 we report on some of the observational data collected on our study population. We focus in particular on an unusual observation of hunting behaviour, which may support the "necessity drives innovation" hypothesis discussed earlier. This chapter therefore relates to my first stated research objective. Following on this observation and anecdotal evidence from other studies, we conducted an experiment to address objective 2. Chapter 3 investigates how neophobia, exploration diversity and persistence interact to influence learning and problem solving using a novel puzzle with several solutions. Chapter 4 brings the preceding chapters together with overall conclusions that may be drawn, and a discussion of possible future directions regarding bat-eared fox cognition research.

1.9. Comments on dissertation’s structure

All data chapters (chapters 2 and 3) were prepared as stand-alone manuscripts suitable for publication. These chapters have been re-formatted to fit into the dissertation conforming to the overall style (Animal Behaviour) used throughout this manuscript. However, due to the stand-alone style of each chapter, there is some degree of overlap in content of each chapter, mainly their introductions, with the content of the general introduction to this dissertation. References have been consolidated in one reference list at the end of the document. At the time of writing, Chapter 2 has been accepted for publication in African Journal of Ecology. All manuscripts were written and prepared by the author of this dissertation, but where co-authors contributed to the content, acknowledgement is given at the start of the chapter.

CHAPTER 2

First report of a myrmecophageous bat-eared fox *Otocyon megalotis* hunting a hare *Lepus sp*.

Paul J. Jacobs and Aliza le Roux. First report of a myrmecophageous bat-eared fox (*Otocyon megalotis*) hunting a hare (*Lepus sp*.). *African Journal of Ecology.*

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2.1. Introduction

Bat-eared foxes (*Otocyon megalotis* Desmarest 1822) are known for insectivory, with their jaws and dentition specialized for a primarily myrmecophageous diet (Clark, 2005). The harvester termite (*Hodotermes mossambicus*) and other invertebrates comprise 90% of the diet, with vertebrates typically forming < 2% of their stomach or scat content (Bothma, 1966; Klare, Kamler, & Macdonald, 2011; Kuntzsch & Nel, 1992). One source reports lagomorph remains in bat-eared fox scats, classifying it as carrion (Stuart, Stuart, & Pereboom, 2003). Whereas bat-eared foxes have been observed to actively hunt murid prey, it appears unlikely that they are capable of hunting larger prey such as lagomorphs, given their large size (1.5–4.5

kg: Stuart & Stuart, 2001) relative to the foxes (3–5.3 kg: Clark, 2005). Further, Andrews and Evans (1983) proposed that bat-eared foxes' specialized dentition and jaw muscles are too weak to hold or kill prey larger than rodents. It may therefore be considered novel and perhaps unexpected that, in this short note, we describe the first direct observation of a bat-eared fox hunting and killing a hare (*Lepus sp.*).

2.2. Methods

This observation is part of an ongoing ecological study of wild bat-eared foxes habituated to the presence of observers on foot, at the Kuruman River Reserve (28°58'S, 21°49'E) in the Northern Cape, South Africa. At the time of this observation, the study population consisted of ten habituated bat-eared foxes (five males, five females). Project data are collected on a nightly basis, with observers using a handheld spotlight and Android Samsung tablet (programmed with Cybertracker software) to collect observational data, following subjects at a distance of 3–5 m for 2 h per observational session.

2.3. Results and discussion

On 14 November 2014, one of the two authors (P.J.J.) was following an adult female bat-eared fox foraging within her usual home range. At 21:37, a hare (genus *Lepus*; species uncertain due to poor lighting conditions) came within close proximity of the fox (2–4 m from the fox; 4–6 m from the observer). The bat-eared fox, partially hidden from view amidst tall grass, immediately gave chase to the lagomorph. The hare appeared to be in fully fit condition, and responded instantaneously to the fox's chase. Over a distance of < 6 m, the hare only switched direction once, and the fox successfully pounced on her prey. She directed her first bite to the hare's neck/throat, but did not instantly kill it, as the hare's vocalizations continued while the fox carried her prey back to the location where the chase began. No 'canid deathshake' (R. Estes, 1991; Kleiman & Eisenberg, 1973) was observed. This suggests that the bat-eared fox killed the hare through suffocation, analogous to the method used by big cats (R. Estes, 1991; Kleiman & Eisenberg, 1973). In a similar observation of a canid hunt, a single black-backed jackal (*Canis mesomelas* Schreber 1775) inflicted a throat bite on an adult impala, (*Aepyceros melampus* Lichtenstein 1812)(Kamler, Foght, & Collins, 2010). The bat-eared fox consumed the hare's limbs whole, after briefly nibbling on the hare's head and ears, then opened up the hare's abdomen using her forepaws. At this time, a male bat-eared fox of the same social group approached and also began eating the hare. No fighting or dominance behaviours were observed between the two foxes, which were familiar with one another. Twenty-eight minutes elapsed from the capture of the hare until the majority of the prey animal was eaten, with only the head, ears and skin left behind. At this stage, the female fox took some body parts away, uneaten, possibly to provision her offspring. Our observation contrasts to some degree with a report by Klare, Kamler and Macdonald (2011), who described that bat-eared foxes specifically avoided the hair, skin and bones of large vertebrate prey remains (carrion) used to bait traps. Although the hare's skin was mostly avoided, both bat-eared foxes consumed limbs (including small bones) whole. It can be assumed as a hypothesis that the female bat-eared fox has had previous experience in hunting hares and applied the strategy of focusing on the energetically valuable limbs and innards, while the male fox also spent time consuming the less rewarding tail.

The foxes' invertebrate prey base (K. Jumbam, unpublished data; (Nel, 1990)) was likely to be ample during the summer season, when this event was observed. We would not therefore have predicted the hunting of large, risky prey, as bat-eared foxes could easily be hurt or maimed while the prey fights back (cf. Mukherjee & Heithaus, 2013). However, this specific individual's motivation levels may have been particularly high, as we observed her with dependent pups less than three weeks after the hare hunt occurred, and she was seen to chase a hare unsuccessfully on at least one more occasion (February 20, 2015). It is likely that her high nutritional need during gestation and/or lactation (Oftedal & Gittleman, 1989) would have driven her to attempt to take more risky prey, as was indeed also the case for lactating black-backed jackals Kamler et al. (2010). These observations establish that, in contrast to prior expectations, bat-eared foxes are capable of hunting animals larger than rodents, namely hares. At this site, interactions between hares and bat-eared foxes are typically neutral, with foxes showing no more than mild interest, or the hare avoiding direct interaction with foxes. However, we have demonstrated here that bat-eared foxes do not have to restrict themselves to eating carrion (i.e. the remains of large vertebrate prey) in the absence of sufficient small prey animals: in over 506 h of observation at this site, we have never observed foxes eating carrion. We therefore advise researchers who rely on nonobservational methods to determine diet, to remain cognizant of the possibility that even small carnivores with insectivorous diets can be opportunistic and take relatively large and agile prey items.

CHAPTER 3

Exploration diversity, neophobia, persistence and their influence on problem solving in bat-eared foxes, *Otocyon megalotis*

3.1. Abstract

The ability to solve novel problems allows animals to cope with environmental change and potentially exploit novel food resources. Despite the important ecological and evolutionary consequences of problem solving, we still know very little about the traits that vary among individuals within a species to make them better problem solvers. Here we examine problem solving in bat-eared foxes in their natural habitat, by presenting a puzzle feeder with three possible solutions. By examining aspects of individual personality types and puzzle solving success, we demonstrate that persistence is important for individuals, allowing them to exhibit a greater diversity of exploratory behaviour. The first encounter with the puzzle (initial neophobia) did not increase the problem solving success in the first trial; however, higher initial neophobia was negatively correlated with problem solving success when all trials were considered. Our results show that trial-and-error learning was the predominant strategy used to initially solve the object manipulation task, which ended with the conditioned behaviour of

using the forepaws to force the lid down by all successful individuals. Our results suggest that the diversity of exploratory behaviours may be dependent on individual persistence, and may allow basic operant conditioning processes to be enough to generate solutions to novel problems.

3.2. Introduction

3.2.1. Exploration, persistence, neophobia and problem solving

Exploration is the degree to which an individual investigates a novel area or object (Benson-Amram & Holekamp, 2012; Biondi et al., 2010; Cole et al., 2011; Réale et al., 2007). Exploration can be quantified in several ways, which includes the time spent in the novel area or object (Webster & Lefebvre, 2001), the amount of space the individual covers (Overington et al., 2011), the number of sides or parts of an object contacted (Biondi et al., 2010) or the sum of dichotomously scored behaviours towards an object (Benson-Amram & Holekamp, 2012). Previous studies have investigated whether exploration was positively correlated with problem solving in different species (Webster & Lefebvre, 2001) and within species (Benson-Amram & Holekamp, 2012; Cole et al., 2011; Overington et al., 2011), with exploration either positively correlated to problem solving success (Benus, Koolhaas, & Van Oortmerssen, 1987; Guillette et al., 2009; Range et al., 2006) or not correlated in any way (Biondi et al., 2010; Cole et al., 2011). The latter, negative results are in contrast to theoretical predictions, as exploratory behaviour –

a reflection of behavioural flexibility – is expected to correlate positively with innovation and problem-solving success (Benson-Amram & Holekamp, 2012; C. E. Parker, 1974).

Persistence is a motivational measure of task-directed engagement, linked to variety of parameters such as feeding motivation and ecological relevance of the task for the species being tested (reviewed by Griffin & Guez (2014)). For example, an animal may be persistent, consistently using a single motor action when trying to solve a problem, but an animal can also be persistent, yet express a large diversity of motor actions while attempting to solve a problem (Griffin & Guez, 2014). Persistence has previously been measured as either the amount of time spent manipulating an experimental task (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012), the duration of a visit, or the number of attempts to solve a puzzle (Griffin & Diquelou, 2015; Morand-Ferron et al., 2011; Morand-Ferron & Quinn, 2011). Persistence has been consistently linked to improved problem solving in animals (reviewed by Griffin and Guez (2014)). For example, in meerkats (*Suricata suricatta*), and spotted hyenas (*Crocuta crocuta*), individuals that spend the most time manipulating experimental tasks solve them most readily (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012). The likelihood of innovative problem solving increased with the duration of visits to the innovation device and the number of previous attempts in tasks presented to great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Morand-Ferron et al., 2011; Morand-Ferron & Quinn, 2011). Individual mynas (*Acridotheres tristis*) and meerkats who were more persistent had shorter solving latencies (Sol, Griffin, & Bartomeus, 2012; Thornton & Samson, 2012).

Neophobia has also influenced problem solving ability (Benson-Amram & Holekamp, 2012; Dugatkin & Alfieri, 2003; Guenther, Brust, Dersen, & Trillmich, 2014; Guillette et al., 2009;

Sneddon, 2003; Tebbich, Sterelny, & Teschke, 2010; Thornton & Samson, 2012; Webster & Lefebvre, 2001). Neophobia is the avoidance of novel stimuli (Benson-Amram & Holekamp, 2012; Bergman & Kitchen, 2009), commonly measured as the latency to approach a novel object (Benson-Amram & Holekamp, 2012). Individuals that are more cautious may perform better at cognitive tasks due to the ability to adjust their behaviour and explore novel situations more thoroughly (Benus et al., 1987; Cole et al., 2011; Verbeek, Drent, & Wiepkema, 1994). In contrast to these views, several studies found neophobic individuals to perform poorly at cognitive tasks, due to the avoidance of novel stimuli (Benson-Amram & Holekamp, 2012; Dugatkin & Alfieri, 2003; Guenther et al., 2014; Guillette et al., 2009; Sneddon, 2003; Webster & Lefebvre, 2001). Alternatively, a few studies have found no correlation of object neophobia and problem solving success (Biondi et al., 2010; Cole et al., 2011). Due to conflicting results as to how neophobia, exploration and persistence interacts with cognitive performance (Carere, 2003; Cole et al., 2011; Guillette et al., 2009; Sneddon, 2003), the relationship between cognitive performance and neophobia, exploration and persistence remains unclear and still constitutes an open topic of investigation (Cole et al., 2011; Hopper et al., 2014).

Bat-eared foxes (*Otocyon megalotis*) have one of the smallest brains in the canid family, with the mean encephalisation quotient of 1.10 compared to a mean of 1.41 of 60 canid species studied (Boddy et al., 2012). Despite the small brain-size, bat-eared foxes are purported to show well-developed cognitive skills related to their complex ecological environment. It has been suggested that foxes use resource mapping of termite mound locations, including knowledge of when these termite mounds are depleted (Lourens & Nel, 1990). This implies that bat-eared foxes should have some degree of proficient memory to recall the location of termite mounds. Bat-eared foxes also exhibit innovative abilities, through the provision of pups with dung that has ensconced insects (le Roux et al., 2013). This is unique as bat-eared foxes were not previously known to provide food to offspring at the den other than milk (Pauw, 2000). To my knowledge the technical problem solving skills in bat-eared foxes has not previously been investigated.

Here, we test whether individuals who are more investigative and display a greater range of investigatory behaviours (henceforth referred to as exploration diversity (ED)) during the solving of a novel puzzle are most likely to eventually solve that problem (Benson-Amram & Holekamp, 2012; Caruso, 1993; C. E. Parker, 1974). Along with ED, we will also investigate the relative influences of neophobia and persistence to problem solving. We predict a positive correlation between persistence and ED, and a negative correlation between ED and neophobia. We also expect that more persistent individuals will be more successful than less persistent individuals. Finally, because learning is necessary for individuals to solve problems, we examine the rate of learning among individuals who were successful at solving the problem. As a consequence of operant conditioning (associative learning), we predict that individuals will solve the puzzle faster with repeated exposure.

3.3. Methods

3.3.1. Subjects and study site

Study subjects came from a wild population of bat-eared foxes in the Kuruman River Reserve (28°58’S, 21°49’E) in the Northern Cape, South Africa. The most habituated individuals were chosen for this study to reduce the possible impact of the presence of an observer on learning speed in less habituated animals. Individuals were sexed based on distinct urination postures (Lamprecht, 1979), and individually identified by unique body scars and/or markings. Eleven individuals (five males, six females) were used in this study. Experiments took place between 18 June 2014 and 3 July 2014, in the late afternoon to evening (between 16:00 and 23:00), when foxes were actively foraging. All individuals were adults or sub-adults (age: above 6 months).

3.3.2. Puzzle box

A 4mm thick Perspex puzzle box (25 cm x 20 cm x 10 cm, weight: 3.2kg) was mounted on a wooden base to prevent flipping of the puzzle (Figure 3.1). The puzzle box was baited with seedless raisins, which individuals could see and smell through the holes in the puzzle box (Figure 3.1). The puzzle box had a swing-bin lid, which could be manipulated by pressing on the lid, a lever or pulling a rope (Figure 3.1), giving test subjects three possible options for opening the box. Attachments could be manipulated by either using the muzzle or the forepaws. With the lid down, the opening was large enough for bat-eared foxes to put their head inside the box and access the reward.

Figure 3.1. The puzzle box used in the experiment.

3.3.3. Experimental procedure

Individuals were located and separated from others to prevent social influence. This was done by keeping all individuals, except the focal individual at least 25m away from the puzzle by distracting them with the food reward by an assistant. All trials were videotaped by an observer using an infrared video camera (Bushnell Equinox Z 4.5 x 40mm) at a distance of 25-30 m from the puzzle box. The experimenter who had placed the puzzle box remained at least 5 m away from the box, and did not interact with the focal individual or the puzzle box once the focal subject noticed it. A trial started once the focal individual directed its attention to the puzzle box and started sniffing it at close proximity or made deliberate contact. A trial ended under three conditions: (1) when an individual ate a raisin from inside the box, (2) moved more than 20 m away, or (3) remained more than 5 m away from the puzzle box for 5 min. Successful trials were defined as opening and eating a raisin inside the puzzle box.

Unsuccessful trials were those where individuals directed attention to the puzzle box (head down looking at it, or direct interaction with the puzzle box), yet failed to open it. A mistrial was defined as when an individual did not approach within 1 m of the puzzle box but spent time within 4 m of the box.

3.3.4. Number of trials per individual

Individual foxes were opportunistically chosen based on who was present on a given day. All individuals received five trials, regardless of success or failure rate, and had at least 22 hours between subsequent trials. The intervals between measurements were 55.69 ± 43.11 h (mean ± SD), ranging from 22.11 to 191.25 h. A total of 58 trials were performed on 11 individuals with three trials repeated due to social interferences.

3.3.5. Data extraction

Video recordings of each trial were analysed by multiple observers. Trials were analysed frame-by-frame until at least two observers agreed on the number of frames per trial determined by a 5% error margin. The 5% error margin was calculated by taking the average of two observers divided by one of the observers from the two. If error margins exceeded 5%, other observers were used until a trial fell within a 5% error margin. All observers were instructed to analyse the videos in the same way by following a protocol to extract the following data: latency to approach, work time (WT) and ED. The puzzle box was an entirely novel stimulus for the bat-eared foxes, thus neophobia was estimated by examining the latency of approach of the focal individual from the moment it entered a two-meter radius around the puzzle box in the initial trial, until the fox was head down, sniffing the puzzle at close proximity or made deliberate contact with the box. However, as no other experiments were conducted to specifically investigate neophobia, the repeatability of neophobia (Réale et al., 2007) could not be determined. Work time was calculated as the total time an individual spent with its head down, fully engaged with the puzzle box, until an end trial condition was met. Movement around the puzzle was included in the WT if the fox's attention was on the puzzle box. Work time was excluded if attention left the puzzle but continued again when attention reverted back to the puzzle. We also quantified exploration for each trial. Similar to Benson-Amram and Holekamp (2012), ED was dichotomously (0/1) scored whether individuals bit, used their paw, pulled any part, or licked the puzzle box. Thus, an individual who performed all four behaviours would be deemed explorative (score = 4) and a score of 0 would be a non-explorative individual.

3.3.6. Statistical analysis

We converted frame data to seconds for all analyses. One individuals' data (neophobia, WT and ED) was an outlier and subsequently excluded as normality could not be obtained, even after log transforming. Exploration diversity and WT were mean-centered for each individual, and other continuous traits were scaled to a mean of zero and a variance of one. First, we fit a model with ED score as a function of sex and trial (the two fixed effects). Individual identity was included as a random effect. This model examined how sex and habituation across trials might impact ED. Second, to test for individual differences in learning we fit a random regression model of work time as a function of sex, trial, ED score, and time between trials. Exploration diversity was included because we were interested in whether exploration allowed individuals to solve the puzzle box sooner. Time between trials (TBT) was also included because individuals that had shorter intervals between trials may remember how to solve the puzzle box and may be able to solve it quicker. Trial was included as a fixed effect because of potential habituation and learning effects. Trial was also nested within individual as a random effect. Random regression models are used to test for covariance between intercept and slope, and in this case we wanted to know whether individuals differed in how quickly they learned to open the box, i.e., among individual differences in work time across trials. We used log-likelihood ratio tests to test the significance of random effects. Because only one random effect was included in the exploration model, we conducted the likelihood ratio test based off simulated distribution values from a linear model fitted with the same fixed effects. To test for individual differences in learning we performed log likelihood ratio tests between the random regression model and models with only random intercepts and one with only random slopes. A significant effect of individual suggests that individuals do act consistently different from one another. We used 95% confidence intervals to assess the significance of fixed effects. Repeatability, or the amount of phenotypic variance attributed to among individual differences, was calculated by dividing the variance attributed to individual over the total phenotypic variance. All analyses (except correlations) were performed in R v.3.2.1 (R Development Core Team, 2015) using the LME4 package (Bates, Maechler, & Bolker, 2012). Log likelihood ratio tests were conducted using the

RLRsim package (Scheipl & Bolker, 2013). Using Pearson correlation tests, latency to approach was correlated with ED, WT, results (solved or unsolved) and overall success (how many of the 5 trials were solved and unsolved) to determine significance. Calculations were all performed in SAS (SAS Institue Inc, 2009).

3.4. Results

3.4.1. Problem-solving and individual learning

Of the 10 individuals who interacted with the puzzle box, eight opened the puzzle box, with six of the eight opening the puzzle box on the first attempt. The other two individuals opened the puzzle box on their second attempt. Trial number was a significant predictor of WT, with decreased WT as trial number increased (Table 3.1), suggesting learning across trials (Figure 3.2). Sex and TBT did not significantly affect WT (Table 3.1). Foxes with higher ED also had higher WT (Table 3.1). Trial number was as a significant predictor of ED, with foxes decreasing in ED as trial number increased (Table 3.2; Figure 3.3). Sex did not significantly affect ED (Table 3.2).

Table 3.1.

Mixed linear model on predictor variables affecting work time

Predictor variables	Estimate±S.E.	Lower CI	Upper CI	p value
Intercept	0.84±0.38	0.093	1. 58	>0.05
Sex	0.27±0.28	-0.28	0.82	>0.05
Trial	**-0.32±0.097**	**-0.51**	**-0.12**	**<0.05**
Exploration diversity	**0.34±0.14**	**0.067**	**0.62**	**<0.05**
Time between trials	-0.05±0.11	-0.27	0.17	>0.05

The model was based on data of all five trials of 10 bat-eared foxes that were successful and unsuccessful. The response variable is log work time. Significance was determined by CI excluding 0. This means if 0 does not fall within the range of the lower CI and the upper CI the predictor variable has a significant effect. Significance is highlighted in bold.

Table 3.2.

Mixed linear model on predictor variables affecting exploration diversity

Predictor variables	Estimate±S.E.	Lower CI	Upper CI	p value
Intercept	0.79±0.37	0.12	1.46	>0.05
Sex	-0.25±0.44	-1.02	0.53	>0.05
Trial	**-0.23±.079**	**-0.38**	**-0.079**	**<0.05**

The model was based on data of all five trials of 10 bat-eared foxes that were successful and unsuccessful. The response variable is exploration diversity. Significance was determined by CI excluding 0 and is indicated in bold. This means if 0 does not fall within the range of the lower CI and the upper CI the predictor variable had a significant effect. Significance is highlighted in bold.

3.4.2. Individual variation and repeatability in exploration diversity and work time

We inquired whether there were consistent individual differences in WT and ED for all 10 individuals used in the analysis. Work time did not differ over time between individuals (likelihood ratio test=2.13, p=0.35). Work time was not repeatable for individuals (repeatability=0.154, likelihood ratio test=0.037, p=0.22). Exploration diversity was significantly repeatable for individuals across trials (repeatability=0.354, likelihood ratio test=5.96, p=0.004). Exploration diversity ranged from individuals with 0 to 3 with no individuals scoring a maximum of 4.

3.4.3. Latency to approach influence on work time, exploration diversity and problem-solving success

Latency to approach was not significantly correlated with WT (Pearson coefficient r=0.29, p=0.48) and not significantly correlated to the trial 1 result (Pearson coefficient r=-0.63, p=0.06). However, overall success was significantly negatively correlated to latency to approach (Pearson coefficient r=-0.85, p=0.02), with no correlation between average ED (individual average) and latency to approach (Pearson coefficient r=-0.39, p=0.29).

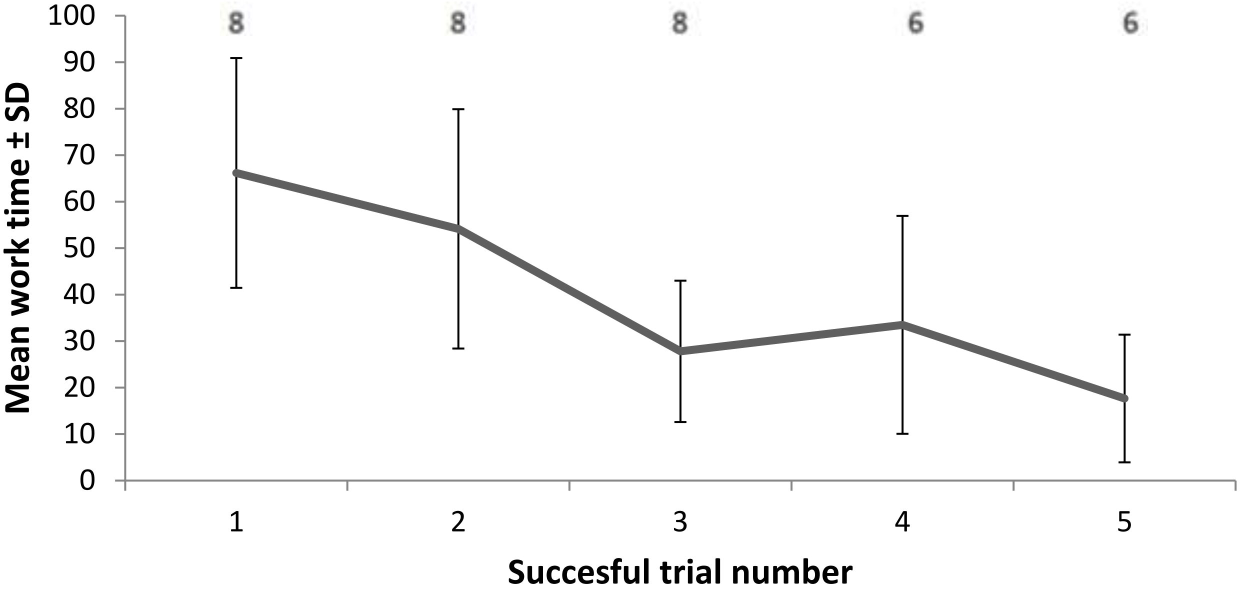

Figure 3.2. Average learning curve for successful wild bat-eared foxes in opening the puzzle box in a given trial. The first "successful" trial represents the trial in which an individual was initially successful, and may not be the first time an individual interacted with the puzzle box. The maximum number of successful trials was 5. The number of successful foxes is outlined above each trial.

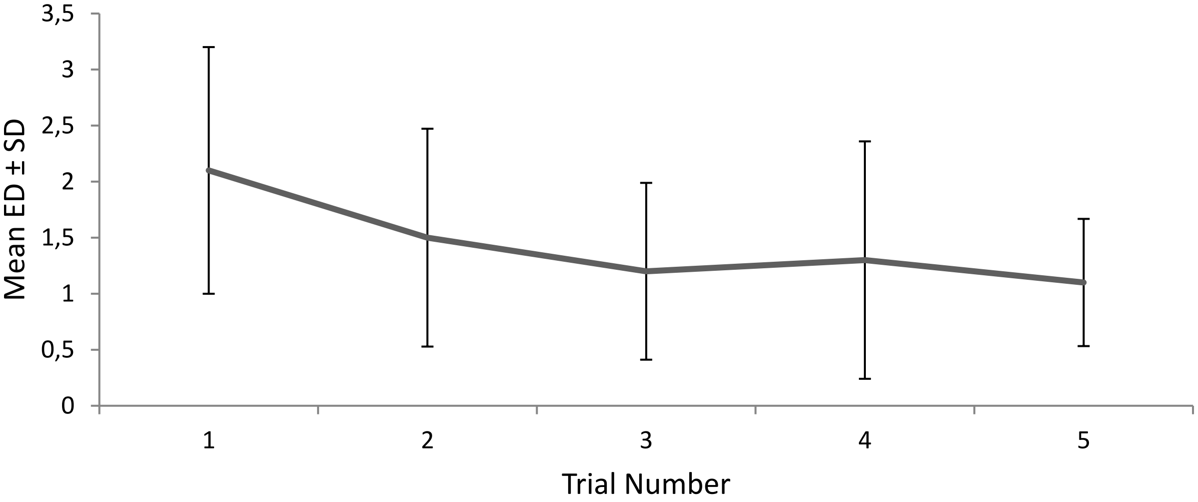

Figure 3.3. The curve represents exploration diversity (ED) for all wild bat-eared foxes that interacted with the puzzle box. Trial number had a significant effect on mean ED trial number.

3.5. Discussion

3.5.1. Exploration diversity, persistence and neophobia influence on problem-solving

In this study, we used work time and latency to approach as proxies for persistence and neophobia, respectively. Exploration diversity (ED) and trial number were significant predictors of persistence, with neophobia negatively influencing overall success rate in bat-eared foxes. Similar to previous studies investigating the number of motor patterns directed towards an object, this study indicates that bat-eared foxes' ED Increased with persistence (Benson-Amram & Holekamp, 2012; Benson-Amram, Weldele, & Holekamp, 2013; Griffin, Diquelou, & Perea, 2014). With no conflicting evidence to date, this study further demonstrates the importance of ED and persistence in problem solving tasks. Our results on neophobia supports the already growing body of studies showing that personality influences problem solving abilities, with higher initial neophobia decreasing problem solving success (reviewed by Griffin & Guez, (2014). Individuals who give up quickly are less likely to be successful than more persistent individuals (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012). Although factors such as body state (translating to motivational differences) may influence the persistence of individuals to obtain a food reward (Réale et al., 2007), Thornton and Samson (2012) and Cole et al. (2011) found that their results on problem solving were not influenced by body state. Since ED was correlated with WT (Table 3.1) and not correlated with success in the initial trial or the average of trials 2-5. One explanation may be that individuals had more opportunities to perform actions that were included in the ED score with increased persistence. Persistence and

ED together may allow individuals to be more flexible in their problem solving ability. Persistence in this study was not repeatable, likely due to a power effect in statistical analysis. This may be due to individuals learning at different speeds, for example, an individual that was better learner may have solved the problem quicker even though they may have taken longer to solve the puzzle box on the first trial.

As expected, once bat-eared foxes learned to open the puzzle box, they became very efficient, demonstrating lower ED and decreased persistence in later trials. However, although only two individuals never solved the puzzle, the behaviour of these two individuals changed as they also demonstrated lower ED as trials progressed. It is possible that the lower ED score and shorter WT in the unsuccessful individuals may have been due to loss in motivation. In order to successfully solve novel problems, individuals must also be willing to engage with unfamiliar objects or situations in the first place (Benson-Amram & Holekamp, 2012). Several studies have found the degree of neophobia to be correlated to problem solving success (Benson-Amram & Holekamp, 2012; Guenther et al., 2014; Sih & Del Giudice, 2012; Sneddon, 2003). Less neophobic individuals are often found to be better problem solvers (Benson-Amram & Holekamp, 2012; Dugatkin & Alfieri, 2003; Guenther et al., 2014; Guillette et al., 2009; Sneddon, 2003; Webster & Lefebvre, 2001), however several studies have found no correlation of object neophobia and problem solving success (Biondi et al., 2010; Cole et al., 2011). This study found that overall success was negatively correlated with higher neophobia. Although a small sample size, both unsuccessful individuals that did not solve the puzzle at all had much higher latency to approach (18.71s) the novel object compared to individuals who were either initially or eventually successful (6.06s).

The effects of high neophobia was only revealed when all trials were considered instead of only the initial trial, thus a higher neophobia may have a long term effect on problem solving ability compared to individuals who are only moderately neophobic. It is possible that the degree of habituation of the animals may have reduced their neophobia of the novel object when experimenters were present. Experiments may require more novel objects, or experiments involving spatial exploration without the presence of experimenters, to more accurately reveal the relationship between ED, neophobia and problem solving. Alternatively, an unsolvable task and a solvable task may better explore the relationship, as although some studies (mostly domestic dogs) have investigated persistence in an unsolvable task (Marshall-Pescini, Valsecchi, Petak, Accorsi, & Previde, 2008; Miller, Pattison, Laude, & Zentall, 2015; Shimabukuro, Putrino, Helbling, Tognetti, & Bentosela, 2015), one study investigated how an unsolvable task may influence problem solving with dogs suffering from anxiety disorders, and found more anxious dogs to be poor problem solvers (Passalacqua, Marshall-Pescini, Merola, Palestrini, & Previde, 2013). In conclusion, although there are costs associated with reduced neophobia such as increased predation risk (Day, Coe, Kendal, & Laland, 2003), our results reveal that less neophobic individuals are better problem solvers than more neophobic individuals.

3.5.2. Problem-solving and individual learning

With regards to learning, our results support the hypotheses that bat-eared foxes could be goal directed and use associative learning to reach their goals. Most individuals were successful in this study with only two individuals not opening the puzzle and two more individuals not opening the puzzle on their first try. Goal directed behaviour is expected to be repeatable because successful behaviour is reinforced by a reward (Skinner, 1938). Bat-eared foxes initially resorted to circling the puzzle and digging close to the holes where individuals could smell and see the food reward. Successful individuals eventually resorted to digging on top of the puzzle resulting in pressing the swing-bin lid down to access the food reward. Unsuccessful individuals only pawed close to the holes where the food reward was and eventually lost motivation. This digging on top of the box by successful individuals was rapidly perfected in opening the puzzle, suggesting trial-and-error learning through associative learning and conditioning. This is supported by the reduction in ED and WT as trials progressed, and the jagged and shallow shape of the learning curve (Figure 3.2), instead of a steep and smooth curve more indicative of "insight-like" learning (Benson-Amram & Holekamp, 2012; Thorndike, 1911; Werdenich & Huber, 2006). Wild mongooses, meerkats and hyenas also resorted to trial-and-error learning to solve novel problems (Kubina, 2014; Müller, 2010; Thornton & Samson, 2012). Even though bat-eared foxes have a likelihood to excel at learning socially (Nel, 1999), this study found that they can easily resort to trial-and-error learning for individual problem solving.

3.5.3. Sex and individual identity influences on exploration diversity, persistence and neophobia

Major factors thought to influence problem solving include sex and individual differences (Boogert et al., 2006; Reader & Laland, 2001; Thornton & Samson, 2012). Previous studies have found sex differences to influence problem solving or individual differences (Bettis & Jacobs, 2009; Hopper et al., 2014; Range et al., 2006; Reader & Laland, 2001; Titulaer et al., 2012); however, this study, along with several other studies(Benson-Amram & Holekamp, 2012; Carere & Locurto, 2011; Cole et al., 2011; Thornton & Samson, 2012), found no influence of sex on problem solving ability or personality. Discrepancies in sexes involving problem solving may result from differences in reproductive effort due to parental investments asymmetries (Laland & Reader, 1999), however in bat-eared foxes the male also invests a lot into parental care suggesting that the discrepancy would be less in this species (Malcolm, 1986), and may explain why no sex differences were observed. To my knowledge discrepancies in parental investments asymmetries have not been tested between species of lower and higher investment for innovative tendencies.

Individual personality types (e.g. neophobia) can only be defined if the type is repeated across different contexts (Réale et al., 2007; Sih et al., 2004; Sih & Del Giudice, 2012). Exploration diversity was repeatable and consistent within all individuals or effects not included in the model. Despite being significant the residual variation (0.62) observed was high, suggesting most of the phenotypic variation observed was within individuals. This means that it was likely that the experimental test did not generate behavioural variation as all individuals may have just reacted the same way to the experimental setup (Réale et al., 2007). It is likely that all individuals have access to the same motor patterns used in the ED investigated and that most individuals will resort to using those behaviours in problem solving. Unfortunately, it was not possible to correctly define each individual’s relative neophobia, as this trait was only measured in one context.

It is suggested that cognitive complexity is linked to intelligence, pointing to correlations between brain size and rates of innovation and problem solving (Dunbar, 1998; Lefebvre et al., 2004; Ramsey et al., 2007; Reader & Laland, 2001; Thornton & Samson, 2012). However, one must be cautious in assuming all problem-solving situations are cognitively demanding. One possible predictor of problem solving success may be individual motivation and persistence (Thornton & Samson, 2012). We suggest that simple trial-and-error associative learning gained through persistence may suffice to generate solutions to relatively simple problems, but more difficult problems may require innovation. It still remains to be tested whether ED correlates with increased learning and flexibility across species and across individuals and future studies are encouraged to investigate these aspects.

CHAPTER 4

Research synthesis and conclusions

4.1. Introduction

This dissertation set out to answer questions about the cognitive performance of bat-eared foxes (*Otocyon megalotis*) in an ecological context. Bat-eared foxes have the smallest brain size amongst canids, yet have shown proficient problem solving abilities. This was observed through a novel behaviour of a female fox hunting a scrub hare and the opening of a puzzle box by several bat-eared foxes. The ecological relevance of these cognitive skills demonstrates that bat-eared foxes can rapidly adjust to new situations in order to acquire food resources. This species therefore offers a unique opportunity to investigate the types of cognitive challenges that can be met by animals with relatively small brains, and allows researchers to perhaps move away from an exclusive focus on relatively large-brained mammals' cognitive skills. This will reveal important questions as potentially identifying the lower limit of cognitive abilities, as well as the cognitive complexity available to smaller-brained animals.

4.2. Innovation?

The first account of a bat-eared fox showing innovation was when a male bat-eared fox provided pups insects that were ensconced in dung (le Roux et al., 2013). In this study, a rare foraging event occurred, most likely, due to a high nutritional need for pup provisioning (Gittleman & Thompson, 1988). Due to the nature of how the scrub hare was devoured by the female bat-eared fox it was likely not a novel behaviour in her own repertoire. However, observation of other foxes attempting to hunt hares interactions suggests two possibilities. The first, that killing and hunting hares is a skill available only this particular female, or this skill is available to all foxes, and that the other foxes had no need to hunt hares or were not given the opportunity. The latter could not be tested as no other foxes were seen to hunt a hare at close proximity, and all other fox-hare interactions remained apparently neutral. The possibility that all foxes could hunt hares remains present, and indirect evidence from other studies (Bothma, 1966; Stuart et al., 2003) suggest that foxes do eat vertebrates of this size. To determine whether this was truly innovation, further fox-hare interactions need to be observed to determine its prevalence in this population of bat-eared foxes.

4.3. Exploration, persistence and neophobia

The present study only investigated the exploration-avoidance personality trait. Recall that personality refers to stable, long-term behavioural, emotional, and physiological differences in suites of traits among individuals of the same species (Carere & Locurto, 2011; Gosling, 2001; Kurvers et al., 2010; Réale et al., 2007; Sih et al., 2004; Webster & Lefebvre, 2001). The context used to determine the influence of personality on problem solving in this study (puzzle manipulation) was limiting and alternative measurements may be necessary. An alternative measurement of personality in a different context include presenting a satiated individual with a novel object and measuring the animal's willingness to approach and interact with the object (Greenberg & Mettke-Hofmann, 2001). Another includes a 'spatial exploration' task, which involves releasing an individual into a novel room and measuring how much of a room it moves through and/or how fast it moves through the room (Cole et al., 2011; Verbeek et al., 1994). This is similar to an open-field test, where an individual is monitored by how it explores a given space and is more applicable to wild animals, as this has been applied to a wild population of yellow-bellied marmots *Marmota flaviventris* (Petelle & Blumstein, 2014; Petelle, Martin, & Blumstein, 2015). The open-field test can be modified to consist a novel area that include novel stimuli or with familiar stimuli presented in a novel manner to test the exploration-avoidance personality trait (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). Applying bat-eared fox personality measurements in this context may be more revealing to determine true personality measurements in this species.

Neophobia significantly reduced problem solving success, where less neophobic individuals were better able to exploit a novel food source such as the raisins provided by solving the puzzle, despite neophilic behaviour posing a higher risk to the individual by increasing exposure to potential threats. In the end being less neophobic would allow individuals to exploit a limited food source over more neophobic individuals. The bold-shy personality trait (assessment of risky situations, but not novel (Réale et al., 2007)), has also been shown to influence problem solving abilities (Sneddon, 2003). Some bat-eared foxes were readily habituated in this field site whereas other bat-eared foxes were less prone to habituation, it is therefore possible that for this specific experiment animals may show differences in risk taking behaviour in the presence of humans, for example, observer and experimenter presence could have minimised the threat of the initial exposure to the puzzle to some extent. Humans have previously been viewed as a human shield against predators due to humans passively deterring predator presence (Nowak, le Roux, Richards, Scheijen, & Hill, 2014) or alter their behaviour when habituated in the presence of humans (McDougall, 2012), for example, chimpanzees (*Pan troglodytes*) and capuchins (*Cebus capucinus*) in long term projects where individuals have been habituated have shown observed-directed behaviour such as threats, play solicitation, watching and throwing objects at observers (Jack et al., 2008; Nishida, Matsusaka, & McGrew, 2009). Future studies should aim investigate neophobia without the presence of observers. This may be difficult for studies involving wild animals, as their movements may not be accurately predicted and thus difficult to put into practise, however, constant video recording of an area known to be used by a focal individual may provide an alternative.

Persistence has previously been found to interfere with measurements of exploration and boldness (Réale et al., 2007). Persistence was difficult to measure and in hindsight requires an experimental design where an unsolvable puzzle is also presented to eliminate luck as a variable. Unsolvable tasks outside of domestic dog research (Marshall-Pescini et al., 2008; Miller et al., 2015; Shimabukuro et al., 2015), has been largely absent to this author's knowledge, with few exceptions (Smith & Litchfield, 2013). In order to properly measure persistence as a measurement in problem solving performance, the use of an unsolvable task should be part of the experimental design. Alternative methods can also include disabling the method previously used to solve a puzzle leaving only alternative options to solve a puzzle. This may lead to more persistent individuals to find the alternative solutions where less persistent individuals would not. Persistence could also be observed from a natural perspective using bat-eared foxes by investigating foraging success, for example, timing the length of each rodent encounter and the success and failure of such encounters. Few studies have investigated the correlation of personality to the fitness of individuals (Réale et al., 2007), and the bat-eared fox provides a model species to investigate the link between personality and fitness in a natural population.

4.4. Conclusion

The goal of the present study was to understand some of the cognitive abilities in bat-eared foxes, such as innovation, problem solving and learning. The results of this dissertation make contributions to the existing knowledge of innovation, problem solving and personality, as well as increasing our basic understanding of bat-eared foxes. Further, identifying other cognitive tests (e.g. memory) may provide further insight to the intelligence of animals that have a small brain for their body size. Lastly, bat-eared foxes can greatly contribute to the rising field of personality and canine cognition, as bat-eared foxes have shown to be readily habituated, allowing for possible longitudinal studies on personality, cognition and fitness.

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