UNIL | Université de Lausanne

Unicentre
CH-1015 Lausanne
http://serval.unil.ch

Year : 2023

Lab cognition going wild

Mohr Tecla

Mohr Tecla, 2023, Lab cognition going wild

Originally published at : Thesis, University of Lausanne

Posted at the University of Lausanne Open Archive http://serval.unil.ch
Document URN : urn:nbn:ch:serval-BIB_F6A5D19EC0328

Droits d'auteur
L'Université de Lausanne attire expressément l'attention des utilisateurs sur le fait que tous les documents publiés dans l'Archive SERVAL sont protégés par le droit d'auteur, conformément à la loi fédérale sur le droit d'auteur et les droits voisins (LDA). A ce titre, il est indispensable d'obtenir le consentement préalable de l'auteur et/ou de l'éditeur avant toute utilisation d'une oeuvre ou d'une partie d'une oeuvre ne relevant pas d'une utilisation à des fins personnelles au sens de la LDA (art. 19, al. 1 lettre a). A défaut, tout contrevenant s'expose aux sanctions prévues par cette loi. Nous déclinons toute responsabilité en la matière.

Copyright
The University of Lausanne expressly draws the attention of users to the fact that all documents published in the SERVAL Archive are protected by copyright in accordance with federal law on copyright and similar rights (LDA). Accordingly it is indispensable to obtain prior consent from the author and/or publisher before any use of a work or part of a work for purposes other than personal use within the meaning of LDA (art. 19, para. 1 letter a). Failure to do so will expose offenders to the sanctions laid down by this law. We accept no liability in this respect.

UNIL | Université de Lausanne
Faculté de biologie
et de médecine

Département d' Ecologie et Evolution

Lab cognition going wild
Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

Faculté de biologie et de médecine
de l'Université de Lausanne

par

Tecla Mohr

Biologiste diplômée Master de l'Université de Neuchâtel

Jury
Prof. Jacqueline Schoumans, Présidente
Prof. Erica van de Waal, Directrice de thèse
Prof. Philippe Christe, Co-directeur de thèse
Prof. Lydia M. Hopper, Experte
Prof. Catherine Crockford, Experte

Lausanne
(2023)

UNIL | Université de Lausanne

Faculté de biologie
et de médecine

Département d' Ecologie et Evolution

Lab cognition going wild

Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

Faculté de biologie et de médecine
de l'Université de Lausanne

par

Tecla Mohr

Biologiste diplômée Master de l'Université de Neuchâtel

Jury
Prof. Jacqueline Schoumans, Présidente
Prof. Erica van de Waal, Directrice de thèse
Prof. Philippe Christe, Co-directeur de thèse
Prof. Lydia M. Hopper, Experte
Prof. Catherine Crockford, Experte

Lausanne
(2023)

UNIL | Université de Lausanne
Faculté de biologie
et de médecine

Ecole Doctorale
Doctorat ès sciences de la vie

Imprimatur

Vu le rapport présenté par le jury d'examen, composé de

Président·e	Madame	Prof.	Jacqueline	**Schoumans**
Directeur·trice de thèse	Madame	Prof.	Erica	**van de Waal**
Co-directeur·trice	Monsieur	Prof.	Philippe	**Christe**
Expert·e·s	Madame	Prof.	Lydia M.	**Hopper**
	Madame	Prof.	Catherine	**Crockford**

le Conseil de Faculté autorise l'impression de la thèse de

Tecla Mohr

Master, Université de Neuchâtel, Suisse

intitulée

Lab cognition going wild

Lausanne, le 3 janvier 2024

pour le Doyen
de la Faculté de biologie et de médecine

Prof. Jacqueline Schoumans

Contents

Acknowledgment

Firstly, I express my gratitude to my supervisor, Erica, for entrusting me with this project and permitting my involvement over the years. Her guidance and assistance have been invaluable throughout this undertaking, and her support has been crucial during the most challenging moments, providing me with the fortitude to conclude this work. I would like to express my gratitude to my two supervisors, Rachel and Charlotte, who supported me throughout the past few years of my thesis. Their guidance was invaluable in terms of both thesis writing and data analysis.

Additionally, I am grateful to the van der Walt family for providing me with an opportunity to work in the idyllic location of Mawana. This wonderful place has been my home for almost six years and I must thank the van der Walt family for accommodating my project. In addition, I would like to express my gratitude to Kallie van der Walt for his invaluable assistance in maintaining the reserve, as well as for all conversations enjoyed in the evenings by the fire. During my stay in Mawana, I was lucky to encounter many delightful individuals, with whom I had the privilege of experiencing profoundly personal and memorable moments. Unknown people who entered the doors of IVP exchanged personal stories with whom I shared unforgettable moments; from enjoying simple aperitifs while watching sunsets on the rooftop, chatting and sharing stories and emotions around the fire during evenings, spending Sundays by the river, to numerous weekends away. These experiences allowed for the formation of strong bonds, which I hope will remain unbreakable. Among these individuals, I wish to express my gratitude to Shannon, Tam, and Millie, who were my angels and were very supportive and helpful to resume data collection after my accident. Additionally, I would like to extend my personal thanks to Arend van de Blerk, with whom I collaborated during the initial months of my thesis, with my sole regret being that we could not have worked together for longer. However, I am most grateful to my esteemed manager, Mike Henshall, for his exceptional leadership. Anyone familiar with Mike knows that he consistently gives 100% effort in his work, as he did for my project. I will forever be thankful to Mike for instilling his passion for wildlife in me, for embarking on countless adventures together in the Kubu territory (rock climbing, step on a puff adder) for his resolute determination and for his instrumental role in the success of IVP. Mike provided stability during my stay and was the person welcomed me back every time with warmly hugs. He acted as a supportive brother, enabling me to complete my project and helping me get through difficult times at IVP. With Mike, I am grateful for two wonderful creatures, Mvula and Ilanga, who served as not only protectors but also warm and friendly companions.

My work was divided between the reserve and sanctuary, and I extend a sincere appreciation to the W.A.T.CH team for their invaluable support in enabling me to work with captive monkeys. I am particularly grateful to our dear Bruce, who served as my mentor and imparted his extensive knowledge of monkeys during my initial year. However, my deepest gratitude goes to my friend Sandy, who has been my South African family and to whom I am indebted for everything. She provided me with the chance to be a temporary mother to young orphaned monkeys - the best experience of my life. She shared her adoration for our Babas and instructed me on caring for others while also taking care of myself. She had faith in me and believed in me even when I didn't believe in myself. Thank you Sandy for the precious moments we shared, the rugby Sundays (go Bookee), and all of our remarkable adventures.

Last but not least, I am grateful to the significant people in my life, my friends and family whom I left in Switzerland. Despite the distance, they supported me throughout my adventure. Their warmth and welcoming nature made my return to Switzerland an enjoyable experience, creating a sense of home. I appreciate their invaluable support during my times of crisis and the affectionate hugs that spoke more than a thousand words. Throughout my thesis, I have been fortunate to receive unwavering support, particularly during moments of great difficulty.

During my thesis I lost my beloved grandmother, who despite the pain of seeing me leave for such long periods of time was always close to me and always supported and understood me, believing in me more than anyone else and she will forever hold a special place in my heart. With immense gratitude and affection, I dedicate this thesis to her memory <3.

Abstract (English)

Many studies have used touchscreens in animal research, however, due to limitations such as the need for electricity, these experiments have only been conducted on captive animals. Despite the development of devices like radio collars and automated systems over the years, there has been a lack of touchscreen adaptations available for the study of wild animals. This project aimed to introduce an innovative starting point for future research with wild animals. The prospect of studying wild animals provides a chance to compare the behaviour and performance of captive and wild animals. The thesis centres on three main topics exploring the potential distinctions between wild and sanctuary animals using touchscreen technology. Chapter 1 analyses the exploratory behaviours of sanctuary and wild monkeys in their first encounter with the touchscreen. Chapter 2 presents the outcome of individual's participation during the entire experimentation period. Towards the conclusion of this chapter, a comparison was made between the performance of wild and sanctuary monkeys during the last third phase of their training. During the final third phase of their training, a blue square was presented on a white screen, and its position changed each time the monkey touched it. Although we found a difference in the participation of the monkeys in the sanctuary and the wild, monkeys in the two contexts (sanctuary vs. wild) did not differ in their performance on a simple associative learning task. In Chapter 3, we tested the abilities of monkeys in the sanctuary to discriminate stimuli in 2D and 3D. We also examined the performance of sanctuary and wild monkeys on two cognitive tests (Match to sample and Reversal learning task) and analysed the potential influence of laterality on individual monkeys. The results indicate two significant findings: firstly, the adaptation of a touchscreen to function in areas with limited access to electricity or mobility is feasible. For instance, reducing the touchscreen's dimensions and weight could lead to the possibility of carrying multiple devices in a collaborative setting. Furthermore, after acquiring proficiency in the touchscreen's use, diverse stimuli can be presented. For instance, by training the monkeys to identify a pattern when it is their turn to interact with the device, it may be possible to regulate the participation of different individuals, resulting in more balanced age and gender as well as rank distributions in future studies. The second objective of this project is to compare sanctuary and wild monkeys' behaviour and cognition. This investigation contributes to the limited number of studies that have analysed performance between sanctuary and wild animals using comparable methodologies, while considering two hypotheses: The Free Time Hypothesis, predicting that animals held in captivity have greater opportunities to interact and explore with the touchscreens, and the enculturation hypothesis which attempts to explain habitual behaviours towards humans' world

such as the touchscreen. This research may inspire future studies to investigate technological innovations including touchscreen technology for testing wild animals, which reflects more natural cognitive abilities while reducing the stress from temporary capture. Furthermore, this project aims to prompt discussions regarding the upkeep of captive animals to ensure their cognitive abilities are maintained and consequently their welfare.

Abstract (French)

De nombreuses études ont utilisé des écrans tactiles dans le cadre de la recherche sur les animaux. Toutefois, en raison de limitations telles que le besoin d'électricité, ces expériences n'ont été menées que sur des animaux en captivité. Malgré le développement de dispositifs tels que les colliers émetteurs et les systèmes automatisés au fil des ans, il y a eu un manque d'adaptations d'écrans tactiles disponibles pour l'étude des animaux sauvages. Ce projet visait à introduire un point de départ innovant pour les futures recherches sur les animaux sauvages. La perspective d'étudier les animaux sauvages permet de comparer le comportement et les performances des animaux captifs et des animaux sauvages. La thèse s'articule autour de trois thèmes principaux qui explorent les distinctions potentielles entre les animaux sauvages et les animaux des sanctuaires à l'aide de la technologie des écrans tactiles. Le chapitre 1 analyse les comportements exploratoires des singes des sanctuaires et des singes sauvages lors de leur première rencontre avec l'écran tactile. Le chapitre 2 présente les résultats de la participation des individus tout au long de la période d'expérimentation. Vers la fin de ce chapitre, une comparaison a été faite entre les performances des singes sauvages et des singes en captivité pendant le dernier tiers de leur entraînement. Au cours de cette dernière phase, un carré bleu était présenté sur un écran blanc et sa position changeait à chaque fois que le singe le touchait. Bien que nous ayons trouvé une différence dans la participation des singes dans le sanctuaire et dans la nature, les singes dans les deux contextes (sanctuaire vs. nature) n'ont pas différé dans leur performance sur une tâche simple d'apprentissage associatif. Dans le chapitre 3, nous avons testé les capacités des singes du sanctuaire à discriminer des stimuli en 2D et en 3D. Nous avons également examiné les performances des singes dans le sanctuaire et sauvages sur deux tests cognitifs (Match-to-sample et Reversal learning task) et analysé l'influence potentielle de la latéralité sur les singes individuels. Les résultats montrent deux choses importantes : premièrement, il est possible d'adapter un écran tactile pour qu'il fonctionne dans des zones où l'accès à l'électricité ou la mobilité sont limités. Par exemple, la réduction des dimensions et du poids de l'écran tactile pourrait permettre de transporter plusieurs appareils dans le cadre d'une collaboration. En outre, après avoir acquis la maîtrise de l'utilisation de l'écran tactile, divers stimuli peuvent être présentés. Par exemple, en entraînant les singes à identifier un modèle lorsque c'est leur tour d'interagir avec l'appareil, il pourrait être possible de réguler la participation de différents individus, ce qui permettrait d'obtenir une répartition plus équilibrée des âges et des sexes ainsi que des rangs dans les études futures. Le deuxième objectif de ce projet est de comparer le comportement et la cognition des singes dans le sanctuaire et des singes sauvages. Cette recherche contribue au nombre limité d'études qui ont analysé

les performances d'animaux captifs et sauvages en utilisant des méthodologies comparables, tout en tenant compte de deux hypothèses: L'hypothèse du temps libre, selon laquelle les animaux en dans le sanctuaire ont plus d'occasions d'interagir et d'explorer les écrans tactiles, et l'hypothèse de l'enculturation, qui tente d'expliquer les comportements habituels à l'égard du monde des humains, tels que les écrans tactiles. Cette recherche pourrait inspirer de futures études sur les innovations technologiques, notamment la technologie des écrans tactiles pour tester les animaux sauvages, qui reflètent des capacités cognitives plus naturelles tout en réduisant le stress lié à la capture temporaire. En outre, ce projet vise à susciter des discussions sur l'entretien des animaux en captivité afin de garantir le maintien de leurs capacités cognitives et, par conséquent, leur bien-être.

1. Introduction

This thesis introduces an innovative project that employs a touchscreen to test primate cognition in a natural environment. The project aims to develop a novel study method utilizing a new technological apparatus to compare cognitive abilities between sanctuary and wild vervet monkeys (*Chlorocebus pygerythrus*). The purpose is to demonstrate the adaptability of studies previously conducted in captivity to a natural setting and to establish a new methodology for future research. Until today, we are not aware of any studies that have integrated touchscreens in the wild, most likely due to limitations in feasibility such as lack power and connection. In this project, we will examine various aspects, such as the animals' initial approach towards the touchscreen, participation of group members, and their performance when completing basic and complex cognitive tasks. We hope that this will provide a starting point for further research to implement the use of touchscreens in the wild.

1.1 Animal cognitive experiments from the past to the present

The term "cognition" refers to the adaptive processing of information, from receiving, information through their five sensory organs, namely eyes, ears, nose, tongue and skin and executing it with functionally appropriate actions (Shettleworth, 2000). Before 1900, psychologists considered cognition to be the ability of humans to solve problems and would compare whether animals from different species were capable of similar feats. Since Darwin, the theory of cognition has expanded from a basic human model to encompass a wider range of animals (Shettleworth, 2009). Romanes' book "Animal Intelligence" (1882) introduced the idea that living beings, from insects to mammals, could develop their own abilities. Inspired by this theory, scientists have tested a broader range of species and behaviours. Ivan Pavlov for example, demonstrated stimuli association in dogs (*Canis lupus familiaris*) in 1903. To test his theory, Pavlov conducted an experiment with dogs by administering two stimuli. First, he rang a bell following in a second time with food. Initially, the dogs did not respond to the bells. Eventually, they linked the two stimuli, and started to salivate solely at the sound of the bell (Pavlov & Thompson, 1902). In the 1930s, researchers discovered through natural observation of blue tits (*Cyanistes caeruleus*) that these birds possessed the skill to forage and open milk bottle lids left outside the door, allowing them to feed on the cream at the edge of the bottle neck (Fisher 1949). While the motivations behind these behaviours were easy to interpret, the question of the mechanism that controlled them remained unresolved. This raises the question as to whether or not animals possess "intelligence". Between the 1930s and 1960s, comparative psychologists conducted animal testing using two approaches:

phylogenetic and ecological. The phylogenetic approach focused on inherited traits and answered questions about the historical relationship among species, their divergences, and common ancestors. Meanwhile, the ecological approach investigated how animals' evolution facilitated adaptation to their natural environment, allowing them to interact with other species, understand ecosystem dynamics, and ultimately enhance survival and reproduction. Kamil and Balda (1989) employed an ecological approach to evaluate the memory capacity of three varieties of birds: Clark's nutcrackers (*Nucifraga columbiana*), pinyon jays (*Gymnorhinus cyanocephalus*) and scrub jays (*Aphelocoma coerulescens*). The results indicated that the memory abilities of nutcrackers and pinyon jays were more accurate than those of scrub jays. These findings demonstrate behavioural variance among the bird populations, which may be linked to differences in their natural environments (Balda & Kamil, 1989). While observing and testing animals in their natural habitat is more valid, there are still factors that could not be controlled, such as sociality, food availability, and the presence of predators. In contrast, laboratory settings allow scientists to manipulate all predictor variables, including light, food, and social interactions, which can influence animal behaviour (Cook, 1993). Captive animals have frequently been subjected to testing in isolated experimental chambers, which are equipped with solid objects, such as cups and strings, and where access to food is restricted in order to control their motivation (Jayne & See 2019. Over the past two decades, studies involving captive animals have investigated various cognitive topics, including tool-use, memory, and numerosity, as well as social cognitive skills, such as communication, cooperation, and social learning (Call et al., 2017; De Waal and Tyack,2009; Haslam, 2013; Roberts, 2019; and Wasserman et al. 2006). Their discovery ranged from fish able to comprehend the size of a shoal (Agrillo & Dadda, 2007), to insects and reptiles being able to acquire knowledge through social learning (Matsubara et al., 2017; Webb, 2012), up to primates' long and short-term memory (Gower, 1992). Numerous psychologists and ethologists have proposed different theories to account for the existence of animal intelligence refers to the cognitive abilities for learning, problem solving by non-human animals. Here, I examine two hypotheses: the Social Intelligence Hypothesis and the Enculturation Hypothesis. The Social Intelligence Hypothesis compares the abilities and brain sizes of social animals with those of solitary individuals. The hypothesis suggests that the demands and challenges of residing within social groups requires advanced cognitive abilities to manage social relationships, anticipate the behaviour of others, and adapt to shifting social dynamics, thus resulting in increased brain development and size in animals (Dunbar, 1998; Jolly, 1966). The Enculturation Hypothesis posits that captive environments induce behavioural and cognitive change in animals, enhancing their tolerance and ability to perform in close proximity to humans (van Schaik & Burkart, 2011). Captivity imposes distinct ecological pressures on animals when contrasted with their natural habitats. Typically, captive groups are smaller, more stable and less intricate than their natural counterparts, owing to variations in group size, proximity, sex ratio, and hierarchy (Price & Stoinski, 2007). When kept in captivity, animals experience social interactions that are divergent from their natural environment. Moreover, the animals tend to seek interaction and communication with human beings (Jayne & See,2019. It is common for captive animals to exhibit abnormal behaviours, which are believed to be a direct consequence of living in an altered habitat (Vonk, 2016). In natural surroundings, exposure to human infrastructure can have both beneficial and detrimental impacts on animals' capacity to adjust to their environment using physical and cognitive capabilities (Lowry et al. 2013). Urban animals, for example, develop their adaptive problem-solving abilities through accessing sustenance from garbage containers (Rössler et al. 2020). On the other hand, the animals' proximity to human infrastructure elevates the likelihood of injuries from factors such as power lines and road traffic, and it decreases their opportunities for natural challenges such as avoiding predators (See review Cope 2022). Researchers have conducted numerous studies in sanctuaries, zoos, and farms where animals reside in safer, more natural social environments. These investigations offer valuable insights into how animals respond to enhanced living conditions, such as problem- solving skills, memory and learning capacity and social interactions. Recently, an increasing number of studies have been conducted in sanctuary environments, across multiple taxa (e.g. parrots, Godinho et al., 2020; and chimpanzees, Cronin et al., 2014). To reduce the impact of human presence during cognitive experiments with free-range animals, researchers utilise diverse devices to minimize interference with the animals' natural behaviour.

1.2 Innovative apparatus: Touchscreens

Prior to the development of touchscreens, researchers used various apparatus to test animals' cognitive abilities. For instance, the semi-automated Wisconsin General Test Apparatus (WGTA) was developed by Harry Harlow and his colleagues in the 1930s as significant advancement in experimental psychology, particularly in investigating learning and problem-solving abilities in non-human primates (Davenport et al., 1970). The apparatus comprised interconnected panels, each presenting distinct challenges, such as retrieving food rewards from behind barriers or solving puzzles. The WGTA was designed to assess cognitive skills through a series of tasks requiring more complex problem-solving abilities. The Wisconsin General Test Apparatus was instrumental in advancing our understanding of primate intelligence and learning processes (Pournelle & Rumbaugh, 1965). The operant chamber built by Skinner in 1930 was another influential tool used in the field of experimental psychology. This chamber was a confined space fitted with buttons or levers where animals could freely move. Skinner hypothesized that animals execute specific actions (e.g. pressing a lever or pushing a button) in response to particular stimuli established. When the animals performed the correct action, they received positive reinforcement in the form of food, while an incorrect action resulted in punishment. The design of the chambers allowed for individual control, enabling manipulation of cognitive abilities such as classical associative learning and memory tasks. In Skinner's experiment, domestic pigeons (*Columba livia*) were exposed to the chambers, which contained two keys of different colours. Subjects were trained to peck one colour and were rewarded with food upon successful pecking (Skinner, 1988). Since Skinner's initial research, the box has undergone modifications based on research requirements, including the addition of stimuli like lights and sounds, as well as recent developments replacing stimuli with images using touchscreen technology (Steurer et al., 2012). There are various benefits related to using touchscreen technology in research. Firstly, it permits the display of multiple visual and auditory stimuli. By using the touchscreen, researchers can be more flexible in generating stimuli and in terms of the location available to exhibit them (Morrison & Brown, 1990). Furthermore, during the trial, participants can interact directly with the stimulus and obtain immediate results from it. Furthermore, the majority of the touchscreen systems have been designed as automatic devices, linked to a food dispenser that minimises the presence of humans. Once inside the room, animals are not in contact with any humans until their session is complete, reducing any potential bias caused by human proximity and ensuring reliable experimental results. To eliminate any human bias, all data is gathered automatically through a computer system, thereby enhancing the accuracy and precision of the information. Through the versatile application of touchscreens, a broad range of cognitive research queries have been investigated, such as numerical memory in chimpanzees (*Pan troglodytes*, Matsuzawa, 1985), discrimination tasks in long-tailed macaques (*Macaca fascicularis,* Schmitt et al.), face recognition in capuchin monkeys (*Cebus apella*, Pokorny & de Waal, 2009) and pigeons (Troje & Bülthoff, 1998), collaboration tasks in dogs and wolves (*Canis lupus*, Dale et al., 2019), and spatial discrimination tasks in red-footed tortoises (*Chelonoidis carbonaria*, Mueller-Paul et al., 2014). The short response time window and rewards make touchscreens an appropriate tool for testing discrimination tasks (Cook et al., 2004; review by Cunha & Renguette, 2022). Finally, touchscreen tasks can be accurately replicated using identical codes and software, aiding comparisons between species worldwide (Dumont et al., 2021). Although the creation of such software requires specialised computer knowledge, once developed, anyone can duplicate the experiment. In 2009, Fagot and Paleressompoulle developed a multi-touchscreen system that can be used simultaneously by multiple guinea baboons (*Papio papio*). The system enhances voluntary participation without isolating individuals from their social group (Fagot & Paleressompoulle, 2009). Over time, touchscreens utilised in zoos and sanctuaries have served as vital tools for the study of animal cognition and have also resulted in an enrichment of animal welfare (Clark et al., 2019; Martin et al., 2022). Zoos and sanctuaries housed different animal species, providing a valuable resource for testing animals that are challenging to maintain in laboratory settings, such as bears (*H. malayanus*, Perdue, 2016), (*Ursus americanus bears*, Vonk & Beran, 2012), bottlenose dolphins (*Tursiops truncates*, Delfour & Marten, 2006), and several primate species such as gorillas (*Gorilla gorilla*, Cronin et al.), Mandrillussphinx sp (Leighty et al., 2011) along with observations made on orangutans (as reviewed by Egelkamp & Ross, 2019). Zoos aim to create a natural environment for animals by providing them with a habitat that closely resembles the wild, including social groups and access to the outdoors. Climbing structures are also provided to enhance the animals' natural abilities, thereby making the experimental results closer to the natural settings (MacDonald & Ritvo, 2016). While zoos have been valued for their ability to enable simple comparisons between species (Hopper et al., 2021; Leinwand et al., 2020), it has recently come to light that tourist and human noises outside enclosures can affect animal behaviour and subsequently their performance (Cronin et al., 2018; Huskisson et al., 2021). The advantages of collaborating with sanctuaries involve the limitation of public access. Additionally, sanctuaries generally house larger populations of conspecific animals in their enclosures than laboratories or zoos, whilst also providing more realistic natural habitats with greater opportunities for social interaction and physical activity. (Lopresti-Goodman & Villatoro-Sorto, 2023).

1.3 Wild vs. Captive

Although, some studies do support the notion that animals in zoos and sanctuary perform comparably to those in laboratory conditions (Gazes et al., 2013), it is important to note that the outcomes can be influenced by factors such as the species studied, the complexity of tasks, and the design of the experiments. Moreover, research suggests that animals in more naturalistic captive environments may outperform their counterparts in traditional laboratory settings in certain cognitive tasks (McCune et al., 2019). Environments that closely mimic natural conditions, providing mental stimulation and opportunities for species-specific behaviours, may contribute to enhanced cognitive performance. While some experiments are conducted in laboratory settings to have a controlled experimental setup, others involve more naturalistic conditions or social settings to observe group dynamics and social learning. It is crucial to recognize that different species exhibit diverse cognitive abilities, and their responses to various testing environments can vary. Some species may adapt well to laboratory conditions, while others may display more natural behaviours and cognitive capabilities in settings that resemble their natural habitats.

When in their natural environment, animals encounter ecological and social constraints, such as sourcing food and finding mates. The intricacy of the information available in this habitat could explain the diverse cognitive skills that wild animals have developed to solve physical and mental problems (Rowell et al., 2021). In contrast to captivity, where group numbers are constrained, animals living in the wild can form their natural social structures which are larger as there are no enclosures to restrain them and they are free to migrate and disperse. Therefore, animals have greater opportunities to enhance their cognitive abilities through learning from other group members, known as social learning (van de Waal et al., 2010). The flow of information can go in different directions depending on the context, like learning from residents an arbitrary food choice, in the case of immigrant animals (van de Waal et al., 2013) and likewise, residents learning from immigrants a novel food resource (Dongre et al., 2021). The gathering of quantitative and qualitative data through natural observations yields insightful information about the social environment, including group size (Morand-Ferron et al., 2011), social interaction abilities (Cole & Quinn, 2012), and social network (Canteloup et al., 2021), which can be quantified and statistically analysed. Individual identification techniques offer greater opportunity for studying wild animals. However, in experiments, individual factors including neophobia (Forss et al., 2021) and social factors such as monopolisation by dominant individuals prevent equally collecting data from all group members (Morand-Ferron et al., 2016). Additionally, the lack of researchers' control over food implies that only motivated subjects are likely to interact with the device (Fagot & Bonté, 2010). These limitations may have discouraged researchers from testing animals in their natural habitat, keeping them in temporary captivity, as in the experiment of Mexican jays (*Aphelocoma wollweberi*, McCune et al.) and meadow voles (*Microtus pennsylvanicus*, Kozuch & McPhee, 2014). The necessity for field experiments has led an increasing number of researchers to conduct such experiments, offering valuable understanding of the adaptive capabilities of wildlife in different environments (Horn et al., 2022). A recent novelty experiment by Forss and colleagues (2021) revealed differences in the number of approaches to novel stimuli between captive and wild vervet monkeys. Wild individuals approached novel stimuli considerably less than captive conspecifics. In a problem solving performance Benson Amram et al.'s

(2013) study evaluated the performance and exploratory behaviours of wild and captive spotted hyenas in response to a novel technical problem. Captive hyenas demonstrated significantly greater success rates and were substantially more curious than their wild conspecifics. In the majority of experiments, captive animals exhibited superior performance compared to their wild conspecifics, with the exception of one study involving great tits (*Parus major*), where captive and wild individuals performed at similar levels (Cauchoix et al., 2017). During this experiment, captive and free-ranging great tits were tested in a successive spatial Reversal Learning Task using an automated apparatus composed of a radiofrequency antenna that automatically recognized subjects, two transparent keys aligned horizontally to display stimuli (LED lights) and collect responses (bird pecks). The birds were required to choose between a left and right key by pecking it. Although wild individuals performed similarly to captive conspecifics, they approached novel stimuli significantly less (Morand-Ferron et al., 2015). Several hypotheses could account for this difference in participation, including the 'free time' or 'excess energy' hypothesis, which suggests that individuals are more likely to participate when they face fewer resource pressures. Captive animals with access to food and water in their enclosures have more free time compared to wild animals who use their time and energy to forage (Kummer & Goodall, 1985). The presence of humans around the apparatus may also influence the motivation of wild animals to approach. To solve these issues, various technological devices have been developed including radio-frequency identification (Aguzzi et al., 2011; Bonter & Bridge, 2011; Fagot & Paleressompoulle, 2009), camera traps (Kays et al., 2010), and thermal imaging (Cilulko et al., 2013). However, we are not aware of any experiments involving touchscreens presented in animals' natural habitat.

The emergence of novel software and technologies offers a potential foundation for testing cognitive abilities in free-living animals using touchscreens. Consequently, this would advance research scope and enable comparison with results from captive populations. Nevertheless, the adoption of such technology in natural settings must be approached with careful ethical considerations, as outlined by Ross et al. (2022). Researchers must carefully assess and address potential impacts on the well-being and natural behaviours of animals, ensuring that the benefits of the research outweigh any potential harm. The use of novel technologies should adhere to ethical guidelines, minimizing stress and disturbance to the animals, and considering the long-term effects on the population and their ecosystem. Ethical considerations play a crucial role in shaping the future of cognitive research in both captive and wild environments, ensuring a responsible and respectful approach to studying the cognitive abilities of non-human animals.

2. Material and methods

2.1 Study site and species

Vervet monkeys are widely distributed throughout southern and eastern parts of Africa and can inhabit a range of habitats, including savannahs, coastal forests, and urban areas. Their habitually open environment and semi-terrestrial ecology permit precise behavioural observations (Mertz et al., 2019). Groups vary in size from 20 to 70 individuals and comprises males and females (Cheney & Seyfarth, 1983). Female vervet monkeys exhibit philopatry, whereas males disperse to other groups upon reaching sexual maturity and change group multiple times throughout their life. The communication system of vervet monkeys has been the focus of numerous studies due to their capacity to differentiate between three diverse alarm calls, each signalling the presence of leopards, eagles, and snakes (Cheney & Seyfarth, 1980).

The wild groups examined in this study were located at the Inkawu Vervet Project (IVP) field site, situated within Mawana Game Reserve, Kwazulu Natal, South Africa (28° 00.327 S, 031° 12.348 E, Figure 1A). The reserve comprises a savannah biome consisting of open grassland, clumped bushveld, and dense acacia and woodland (Mucina & Rutherford, 2006). Since 2010, four groups (AK, BD, LT, NH) have been habituated to human presence and have been monitored regularly by research and field assistants. Between 2014 and 2016, two additional groups (CR and KB) were included in the study population. With the exception of three groups (AK, BD, and KB) that have their home ranges situated near the reserve fence and the LT group, who resides near the owner's house, the rest of the groups have no interaction with humans apart from the researchers (see Figure 1B). Some prior experiments have been conducted within the same groups concerning novelty (Forss et al., 2021), an associative learning task utilising wooden boxes (Borgeaud & Bshary, 2018; García et al., 2021), and social learning (Bono et al., 2018; Botting et al., 2018; Canteloup et al., 2021; Canteloup et al., 2020; van de Waal et al., 2013, van de Waal et al., 2015). The proximity of the field house, and familiarity with field experiments using various apparatus render IVP vervets an ideal population for conducting touchscreen experiments in the wild. The IVP field site provides an advantageous setting for studying monkeys because all six wild groups are observed daily by experienced field assistants Each monkey is identified through distinctive facial features, scars, and notches on their ears. For my project the presence of tall trees and thick vegetation at the sleeping sites provided an ideal setting for safely conducting experiments on monkeys. In addition, once the monkeys settled in at sunset, they would not move until the following day. It was essential to determine the sleeping site location of each group before departing for my experiment. Firstly, due to the weight of the apparatus being 15 kilograms, the chosen location needed to be nearby the road or in a location that was easily and quickly accessible. Additionally, during the summer season, it became impractical to access sleeping sites located on the other side of the river, which often became flooded. Another natural hindrance that could have impacted the execution of the experiment was precipitation. Experiments were restricted in the absence of sheltered installations, with no testing on rainy days. Despite the metal box protecting the touchscreen and all of its components, rainy weather presented a significant issue for the system. The device, being sensitive to humidity, was impossible to protect during wet conditions and therefore could not be used. Additionally, the iPad was highly susceptible to elevated temperatures, malfunctioning when exposed to 35 degrees above temperatures. After encountering the dense vegetation and the river, it was crucial to identify an appropriate location for placing the touchscreen. The device was fastened to the base of a tree with a rope, enabling opportunistic interaction between monkeys and touchscreen. Ensuring that the screen was free from the sun's glare was the primary consideration when selecting the location. In an inappropriate spot, the screen not only reflected the sun but also the image of the monkey positioned in front of it. Previous research findings suggest that monkeys are unable to differentiate their own image (Roma et al., 2007). Observing their reflection can elicit fear in them since they might misunderstand their own reflection as another primate facing them. For this reason, the touchscreen was positioned within a densely vegetated area, close to tall trees that provide optimal conditions for reducing screen reflection. As the experiment was controlled using a remote iPad, the researcher was required to remain within a distance of six metres from the touchscreen. Therefore, while the vegetation was crucial for the monkeys' sense of security, it could not be too dense as it would impede the observer's proximity to the device.

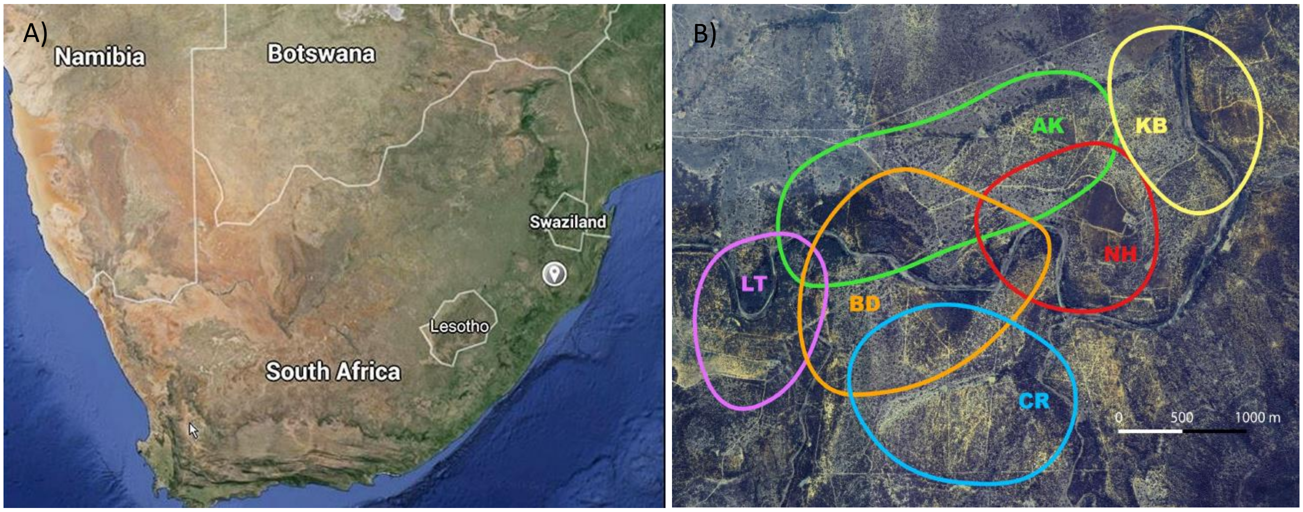


Figure. 1 A: Map of South Africa with a pin on the location of Mawana Game reserve. B: Aerial picture of IVP research area with the approximate home range of the six habituated groups (Dongre Phd Thesis 2022).

The sanctuary groups tested in this study were situated at the Wild Animal Trauma Centre and Haven (W.A. T. C. H.), located in Vryheid, Kwazulu Natal, South Africa. W. A. T. C. H. is a non-profit organization that has been focused on the rescue and rehabilitation of vervet monkeys since 2002. It has sheltered over 300 rescued animals to date and annually rescues orphans and injured monkeys from both rural and urban areas as well as roads. At W. A. T. C. H., monkeys were housed in six enclosures comprised of mixed social groups within an open area, isolated from human interaction. The centre consists of six cages which are furnished with objects such as ropes, wood platforms, tires or trees to enhance the welfare of the sanctuary monkeys (refer to Figure. 2). Daily, the staff members assigned to the centre are accountable for cleaning the cages and providing food and water. Apart from these caretaking measures, monkeys do not have any interaction with human. During my project, I have tested four sanctuary vervet monkey groups (Boeta, Cowen, Liffie and Poena groups). Group composition varied from three to 25 individuals consisting of both males and females aged between three months and five years, except for the Boeta's group, who cannot be released, individuals can attain the age of 16-17 years. The period of three months is regarded as the time in which a rescued baby becomes independent and no longer requires the presence of humans. Except for three old individuals in Boeta's group all remaining groups were kept at the centre for five years before being released into the wild. The group's size and composition are contingent on the individuals rescued over the year and their backgrounds, encompassing orphans, monkeys rescued from roadsides or street-markets, injured individuals or others kept as pets. Researchers have used W. A. T. C. H. to conduct social learning experiments (van de Waal et al., 2013; van de Waal & Whiten, 2012) and also for pilot testing other experiments before conducting them in the wild. Recently, both Boeta and Poena's group had been tested in a comparative study on curiosity in wild and sanctuary populations using a novel objects experiments (Forss et al., 2021).

The methodology in our project was consistent for all three study groups. Following the attachment of the apparatus to the fence, monkeys were free to approach in groups or individually according to their preference. As multiple members of each group tended to approach at the same time, automatic data collection became challenging. To overcome this obstacle and limit the number of individuals in front of the touchscreen, a tunnel within the enclosure was build. We constructed a tunnel using interwoven wires, facilitating visual observations, enabling all monkeys to learn via social learning. The touchscreen tunnel was already installed in Cowen's group during the initial exposure. As this new limitation could have potentially influenced their approach behaviours, I made the decision to exclude Cowen's data from the Chapter 1 analysis.

At W. A. T. C. H., monkeys were housed in six enclosures comprised of mixed social groups within an open area, isolated from human interaction. However, the enclosures lacked any protection for the touchscreen device, necessitating constant movement of the device between groups, causing wastage of time. For each experiment It was necessary for the researcher to be present in order to identify which monkeys were engaging with the touchscreen. Additionally, due to the open area, all experimentation was conducted in the late afternoon, which curtailed the reflective capacity of the screen. The challenge of testing the monkeys in the afternoon was to not modify the sanctuary's routine, including for example the addition of peanuts to the monkeys' diet, which could demotivate them from interacting with the touchscreen. This was due to them undergoing stressful situations in the morning or a few hours prior to my arrival, such as transferring groups to a new enclosure, introducing babies into groups, removing individuals from their groups, and working on the enclosure's maintenance. On several occasions, I was unable to conduct tests on the monkeys. Whenever a stressful situation was caused by human intervention, I avoided conducting the experiment as I did not want it to impact the individuals' performance.

Figure. 2: Image taken at W. A. T. C. H. One enclosure equipped with ropes, tires, trees, platforms, wooden poles and food.

2.2 Summary of chapters

Chapter 1: Introducing touchscreen technology: a comparison of wild and captive vervet monkeys' first approach to a new apparatus

Introducing new objects, researchers have observed neophobic and exploratory behaviours. Previous studies have shown that the context and personality of animals can affect exploratory behaviours (Benson Amram et al., 2013; Bergman & Kitchen, 2009; Forss et al., 2021). This study presents the introduction of touchscreens to both wild and sanctuary vervet monkeys, a novel approach in this area of research. The objective of the study is to utilise a touchscreen as a novelty and compare sanctuary and wild animals in terms of their latency to approach the touchscreen, the duration of time spent interacting with it, and the type of exploration undertaken, analysing both hand and mouth explorations. Our results suggest that sanctuary animals will exhibit a higher likelihood of approaching the touchscreen, spend more time interacting with it, and ultimately display more exploratory behaviours than their wild counterparts. Additionally, wild adults dedicated more time to engaging with the touchscreen than juveniles; and sex played a significant role, with female monkeys monopolising and exploring the touchscreen more than males. The findings corroborate our initial and secondary hypotheses, as sanctuary monkeys showed a quicker approach and extended interaction with the touchscreen in comparison to their counterparts in the wild. However, our results did not detect any variance in exploratory behaviour rates between hand and muzzle usage. Across both the sanctuary and the natural environment, monkeys favoured hand exploration over muzzle exploration.

Chapter 2: Lab cognition going wild: Implementing a new portable touchscreen system in vervet monkeys

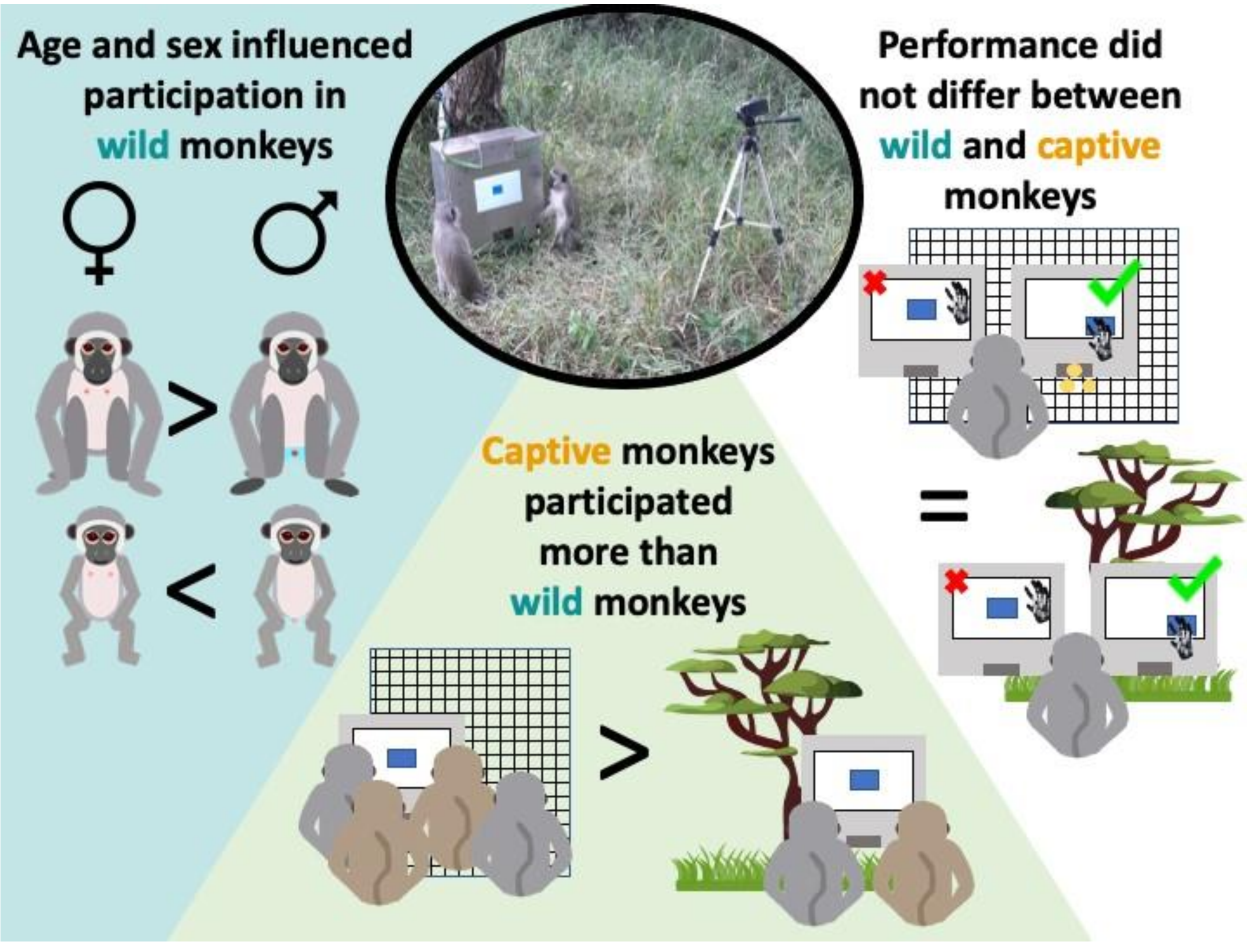


Figure. 3: Results from Chapter 3 on individuals' probability of interacting with the touchscreen, their frequency of participation, and their performance on a simple associative learning task. The study found that sanctuary monkeys participated more than their wild counterparts, whose participation was influenced by sex and age. In the wild, adult females were more likely to participate than males, while juvenile males were more likely to participate than juvenile females. Despite differences in participation, the performance of sanctuary and wild monkeys did not vary.

Chapter 3: "Mind Games: Unraveling the Puzzle of Manual Lateralisation and Stimuli Dimensionality in Vervet Monkeys

Although cognitive experiments using touchscreens have increased in laboratory animals, zoo and sanctuary animals, there is still a lack of knowledge about how 2D stimuli are perceived compared to 3D experimental setups. The stimuli presented on either side of the screen require precise touching by the monkeys. Previous experiments indicate that primates possess manual lateralisation when solving problems. We conducted a discrimination task using images and objects to investigate if sanctuary vervet monkeys perform equally when exposed to stimuli of varying dimensions. Furthermore, we assessed the performance of three wild and three sanctuary groups on both match-to-sample and Reversal Learning Tasks using a touchscreen apparatus to compare their abilities and determine if the body part used influences success rates. Only four out of 17 individuals met the learning criterion with both dimensional stimuli, although they all needed more trials to complete the touchscreen discrimination task. The performance to pass the touchscreen Match-to-Sample task remained unaffected by age and sex, but it was marginally influenced by context. In comparison to wild monkeys, sanctuary monkeys tended to solve the task faster. Participants who used their left hand during the task were more likely to successfully touch the correct stimulus when it was presented on the right side of the screen. However, we did not observe any significant difference in performance when it came to passing the Reversal Learning Task. It is important to note that these results must be interpreted with caution due to the small sample size.

References

Agrillo, C., & Dadda, M. (2007). Discrimination of the larger shoal in the poeciliid fish Girardinus falcatus. *Ethology Ecology & Evolution, 19*(2), 145-157.

Aguzzi, J., Sbragaglia, V., Sarriá, D., García, J. A., Costa, C., del Río, J., Sardà, F. (2011). A new laboratory radio frequency identification (RFID) system for behavioural tracking of marine organisms. *Sensors, 11*(10), 9532-9548.

Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. *Animal behaviour, 38*(3), 486-495.

Beach, F. A. (1950). The snark was a boojum. *American Psychologist, 5*(4), 115.

Benson Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta. *Animal behaviour, 85*(2), 349-356.

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (Papio ursinus) and geladas (Theropithecus gelada). *Animal cognition, 12*(1), 63-73.

Bono, A. E., Whiten, A., van Schaik, C., Krützen, M., Eichenberger, F., Schnider, A., & van de Waal, E. (2018). Payoff-and sex-biased social learning interact in a wild primate population. Current Biology, 28(17), 2800-2805. e2804.

Bonter, D. N., & Bridge, E. S. (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology, 82*(1), 1-10.

Borgeaud, C., & Bshary, R. (2018). Testing for anticipation of partners' reciprocity and other social parameters: An experimental approach in wild vervet monkeys (Chlorocebus pygerythrus). *Journal of Comparative Psychology, 132*(4), 464.

Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. Animal behaviour, 136, 1-12.

Call, J. E., Burghardt, G. M., Pepperberg, I. M., Snowdon, C. T., & Zentall, T. E. (2017). *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior, Vol. 1*: American Psychological Association.

Canteloup, C., Borgeaud, C., Wubs, M., & van de Waal, E. (2019). The effect of social and ecological factors on the time budget of wild vervet monkeys. Ethology, 125(12), 902-913.

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. Nature communications, 11(1), 1-10.

Canteloup, C., Puga-Gonzalez, I., Sueur, C., & van de Waal, E. (2021). The consistency of individual centrality across time and networks in wild vervet monkeys. *American Journal of Primatology, 83*(2), e23232.

Canteloup, C., Cera, M. B., Barrett, B. J., & van de Waal, E. (2021). Processing of novel food reveals payoff and rank-biased social learning in a wild primate. *Scientific reports, 11*(1), 9550.

Cauchoix, M., Hermer, E., Chaine, A., & Morand-Ferron, J. (2017). Cognition in the field: comparison of reversal learning performance in captive and wild passerines. *Scientific reports, 7*(1), 1-10.

Cheney, D. L., & Seyfarth, R. M. (1985). Vervet monkey alarm calls: manipulation through shared information? *Behaviour, 94*(1), 150-166.

Cilulko, J., Janiszewski, P., Bogdaszewski, M., & Szczygielska, E. (2013). Infrared thermal imaging in studies of wild animals. *European Journal of Wildlife Research, 59*, 17-23.

Clark, F. E., Gray, S. I., Bennett, P., Mason, L. J., & Burgess, K. V. (2019). High-tech and tactile: Cognitive enrichment for zoo-housed gorillas. *Frontiers in psychology, 10*, 1574.

Cole, E. F., & Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences, 279*(1731), 1168-1175.

Cook, R. G. (1993). The experimental analysis of cognition in animals. *Psychological Science, 4*(3), 174-178.

Cook, R. G., Geller, A. I., Zhang, G.-R., & Gowda, R. (2004). Touchscreen-enhanced visual learning in rats. *Behavior Research Methods, Instruments, & Computers, 36*(1), 101-106.

Cope, H. R., McArthur, C., Dickman, C. R., Newsome, T. M., Gray, R., & Herbert, C. A. (2022). A systematic review of factors affecting wildlife survival during rehabilitation and release. *PloS one, 17*(3), e0265514.

Cronin, K. A., Bethell, E. J., Jacobson, S. L., Egelkamp, C., Hopper, L. M., & Ross, S. R. (2018). Evaluating mood changes in response to anthropogenic noise with a response-slowing task in three species of zoo-housed primates. *Animal Behavior & Cognition, 5*(2), 209-221.

Cunha, J. M., & Renguette, C. C. (2022). *A Framework for Training Animals to Use Touchscreen Devices for Discrimination Tasks.* Paper presented at the Proceedings of the Ninth International Conference on Animal-Computer Interaction.

Dale, R., Palma-Jacinto, S., Marshall-Pescini, S., & Range, F. (2019). Wolves, but not dogs, are prosocial in a touch screen task. *PloS one, 14*(5), e0215444.

Davenport, J. W., Chamove, A. S., & Harlow, H. F. (1970). The semiautomatic Wisconsin general test apparatus. *Behavior Research Methods & Instrumentation, 2*(3), 135-138.

De Waal, F. B., & Tyack, P. L. (2009). *Animal social complexity: intelligence, culture, and individualized societies*: Harvard University Press.

Delfour, F., & Marten, K. (2006). Lateralized visual behavior in bottlenose dolphins (Tursiops truncatus) performing audio–visual tasks: The right visual field advantage. *Behavioural processes, 71*(1), 41-50.

Dongre, P. (2022). *Integrating dispersal and social learning in vervet monkeys (Chlorocebus pygerythrus).* éditeur non identifié.

Dumont, J. R., Salewski, R., & Beraldo, F. (2021). Critical mass: The rise of a touchscreen technology community for rodent cognitive testing. *Genes, Brain and Behavior, 20*(1), e12650.

Dunbar, R. I. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 6*(5), 178-190.

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology, 38*(2), 220-235.

Fagot, J., & Bonté, E. (2010). Automated testing of cognitive performance in monkeys: Use of a battery of computerized test systems by a troop of semi-free-ranging baboons (Papio papio). *Behavior research methods, 42*, 507-516.

Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior research methods, 41*(2), 396-404.

Fisher, J. (1949). The opening of milkbottles by birds. *Brit. Birds, 42*, 347-357.

Forss, Motes-Rodrigo, A., Dongre, P., Mohr, T., & van de Waal, E. (2021). Captivity and habituation to humans raise curiosity in vervet monkeys. *Animal cognition*, 1-12.

García, M. G., Farine, D. R., Brachotte, C., Borgeaud, C., & Bshary, R. (2021). Wild female vervet monkeys change grooming patterns and partners when freed from feeding constraints. *Animal behaviour, 181*, 117-136.

Gazes, R. P., Brown, E. K., Basile, B. M., & Hampton, R. R. (2013). Automated cognitive testing of monkeys in social groups yields results comparable to individual laboratory-based testing. *Animal cognition, 16*, 445-458.

Godinho, L., Marinho, Y., & Bezerra, B. (2020). Performance of blue-fronted amazon parrots (Amazona aestiva) when solving the pebbles-and-seeds and multi-access-box paradigms: ex situ and in situ experiments. *Animal cognition, 23*(3), 455-464. Gower, E. (1992). Short-term memory for the temporal order of events in monkeys. *Behavioural brain research, 52*(1), 99-103.

Haslam, M. (2013). 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1630), 20120421.

Hopper, L. M., Allritz, M., Egelkamp, C. L., Huskisson, S. M., Jacobson, S. L., Leinwand, J. G., & Ross, S. R. (2021). A comparative perspective on three primate species' responses to a pictorial emotional stroop task. *Animals, 11*(3), 588.

Horn, L., Cimarelli, G., Boucherie, P. H., Šlipogor, V., & Bugnyar, T. (2022). Beyond the dichotomy between field and lab—the importance of studying cognition in context. *Current Opinion in Behavioral Sciences, 46*, 101172.

Huskisson, S. M., Ross, S. R., & Hopper, L. M. (2021). Do zoo visitors induce attentional bias effects in primates completing cognitive tasks? *Animal cognition, 24*(3), 645-653.

Jayne, K., & See, A. (2019). Behavioral research on captive animals: scientific and ethical concerns. In *Animal Experimentation: Working Towards a Paradigm Change* (pp. 517-547): Brill.

Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence: The step from prosimian to monkey intelligence probably took place in a social context. *Science, 153*(3735), 501-506.

Kays, R., Tilak, S., Kranstauber, B., Jansen, P. A., Carbone, C., Rowcliffe, M. J., . . . He, Z. (2010). Monitoring wild animal communities with arrays of motion sensitive camera traps. *arXiv preprint arXiv:1009.5718*.

Kozuch, A. E., & McPhee, M. E. (2014). Effects of environmental complexity and temporary captivity on foraging behavior of wild-caught meadow voles. *Journal of Applied Animal Welfare Science, 17*(2), 157-171.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 308*(1135), 203-214.

Leighty, K. A., Maloney, M. A., Kuhar, C. W., Phillips, R. S., Wild, J. M., Chaplin, M. S., & Betting, T. L. (2011). Use of a touchscreen-mediated testing system with mandrill monkeys. *International Journal of Comparative Psychology, 24*(1).

Leinwand, J. G., Huskisson, S. M., Egelkamp, C. L., & Hopper, L. M. (2020). Within-and between-species variation in the responses of three primate species to a touchscreen gambling task. *Learning and motivation, 71*, 101635.

Lopresti-Goodman, S. M., & Villatoro-Sorto, B. (2023). The Benefits and Challenges of Conducting Primate Research in Different Settings. *Animals, 13*(1), 133.

Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological reviews, 88*(3), 537-549. MacDonald, S. E., & Ritvo, S. (2016). Comparative cognition outside the laboratory. *Comparative Cognition & Behavior Reviews, 11*.

Martin, C. F., Biro, D., & Matsuzawa, T. (2014). The Arena System: a novel shared touch-panel apparatus for the study of chimpanzee social interaction and cognition. *Behavior research methods, 46*(3), 611-618.

Matsubara, S., Deeming, D. C., & Wilkinson, A. (2017). Cold-blooded cognition: new directions in reptile cognition. *Current Opinion in Behavioral Sciences, 16*, 126-130.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature, 315*(6014), 57-59.

McCune, K. B., Jablonski, P., Lee, S.-i., & Ha, R. R. (2019). Captive jays exhibit reduced problem-solving performance compared to wild conspecifics. *Royal Society open science, 6*(1), 181311.

Mertz, J., Surreault, A., van de Waal, E., & Botting, J. (2019). Primates are living links to our past: The contribution of comparative studies with wild vervet monkeys to the field of social cognition. *Cortex, 118*, 65-81.

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

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: associative learning in wild great tits. *PloS one, 10*(8), e0133821.

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological reviews, 91*(2), 367-389.

Morrison, S. K., & Brown, M. F. (1990). The touch screen system in the pigeon laboratory: An initial evaluation of its utility. *Behavior Research Methods, Instruments, & Computers, 22*(2), 123-126.

Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*: South African National Biodiversity Institute.

Mueller-Paul, J., Wilkinson, A., Aust, U., Steurer, M., Hall, G., & Huber, L. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (Chelonoidis carbonaria). *Behavioural processes, 106*, 187-192.

Pavlov, I. P., & Thompson, W. (1902). The work of the digestive glands: lectures by Professor JP Pawlow.

Perdue, B. M. (2016). The effect of computerized testing on sun bear behavior and enrichment preferences. *Behavioral Sciences, 6*(4), 19.

Price, E. E., & Stoinski, T. S. (2007). Group size: Determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied animal behaviour science, 103*(3-4), 255-264.

Pokorny, J. J., & de Waal, F. B. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences, 106*(51), 21539-21543.

Pournelle, M. B., & Rumbaugh, D. M. (1965). A modified Wisconsin General Test Apparatus for use with a variety of small primates. *Perceptual and Motor Skills, 21*(2), 489-490.

Roberts, W. A. (2019). The role of context in animal memory. *Learning & Behavior, 47*, 117-130.

Roma, P. G., Silberberg, A., Huntsberry, M. E., Christensen, C. J., Ruggiero, A. M., & Suomi, S. J. (2007). Mark Tests for mirror self-recognition in capuchin monkeys (Cebus apella) trained to touch marks. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 69*(9), 989-1000.

Romanes, G. J. (1882). *The scientific evidences of organic evolution*: Macmillan and Company.

Ross, S. R., Leinwand, J. G., & Hopper, L. M. 22 Ethical Considerations in Conducting Primate Cognition Research.

Rössler, T., Mioduszewska, B., O'Hara, M., Huber, L., Prawiradilaga, D. M., & Auersperg, A. M. (2020). Using an Innovation Arena to compare wild-caught and laboratory Goffin's cockatoos. *Scientific reports, 10*(1), 1-12.

Rowell, M. K., Pillay, N., & Rymer, T. L. (2021). Problem solving in animals: proposal for an ontogenetic perspective. *Animals, 11*(3), 866.

Rubio, F. (2019). A Cognitive Task as Enrichment for Chimpanzees (Pan troglodytes) in Sanctuary. Schmitt, V., Federspiel, I., Eckert, J., Keupp, S., Tschernek, L., Faraut, L., . . . Bugnyar, T. (2016). Do monkeys compare themselves to others? *Animal cognition, 19*(2), 417-428.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science, 210*(4471), 801-803.

Shettleworth, S. J. (2000). Modularity and the evolution of cognition. *The evolution of cognition, ed. CM Heyes & L. Huber*, 43-60.

Shettleworth, S. J. (2009). *Cognition, evolution, and behavior*: Oxford university press.

Skinner, B. F. (1988). Preface to the behavior of organisms. *Journal of the Experimental Analysis of Behavior, 50*(2), 355.

Steurer, M. M., Aust, U., & Huber, L. (2012). The Vienna comparative cognition technology (VCCT): an innovative operant conditioning system for various species and experimental procedures. *Behavior research methods, 44*, 909-918.

Troje, N. F., & Bülthoff, H. H. (1998). How is bilateral symmetry of human faces used for recognition of novel views? *Vision Research, 38*(1), 79-89.

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science, 340*(6131), 483-485.

van De Waal, E., & Bshary, R. (2010). Contact with human facilities appears to enhance technical skills in wild vervet monkeys (Chlorocebus aethiops). *Folia Primatologica, 81*(5), 282-291.

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences, 277*(1691), 2105-2111.

van de Waal, E., Claidière, N., & Whiten, A. (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. Animal cognition, 18(3), 617-627.

van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 1008-1016. Vonk, J. (2016). Advances in animal cognition. In (Vol. 6, pp. 27): MDPI.

Vonk, J., & Beran, M. J. (2012). Bears 'count'too: quantity estimation and comparison in black bears, Ursus americanus. *Animal behaviour, 84*(1), 231-238.

Wasserman, E. A., Wasserman, E. A., & Zentall, T. R. (2006). *Comparative cognition: Experimental explorations of animal intelligence*: Oxford University Press, USA.

Webb, B. (2012). Cognition in insects. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2715-2722.

Title Chapter 1:

Introducing touchscreen technology: a comparison of wild and captive vervet monkeys' first approaches to a new apparatus

Tecla Mohr [a, b, c] *, Rachel A. Harrison[b, c, f], Charlotte Canteloup [a, b, c, d] & Erica van de Waal [a,b,c, e]

[a] Inkawu Vervet Project, Mawana Game Reserve, South Africa

[b] Department of Ecology & Evolution, University of Lausanne, Lausanne, Switzerland

[c] The Sense Innovation and Research Center, Lausanne and Sion, Switzerland

[d] Laboratory of Cognitive & Adaptive Neurosciences, UMR 7364, CNRS, University of Strasbourg, France

[e] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal,

Pietermaritzburg, South Africa

[f] Swiss Centre for Affective Sciences, University of Geneva, Geneva Switzerland

* Corresponding author: mohr.tecla@gmail.com (TM)

Abstract

Various experiments have explored animal cognition through the use of tools like artificial fruits, automated boxes, and touchscreens. However, it remains unclear whether animals living in the wild and those in captivity show similar levels of interest in these testing apparatuses. The enculturation hypothesis suggests that captive animals who are frequently exposed to humans may be more curious and self-assured when encountering new objects in their environment, leading them to interact with these objects more quickly. To explore this theory, we compared the initial interactions of three groups of wild vervet monkeys (*Chlorocebus pygerythrus*), with two groups of sanctuary vervet monkeys using a novel touchscreen. This study examined exploration behaviour in sanctuary and wild monkeys, categorizing actions into hand and muzzle actions. The goal was to compare approach time, interaction time, and exploration behaviour between the two populations. Our hypothesis predicted that sanctuary monkeys would approach faster, spend more time interacting, and explore more with their hands compared to wild monkeys. The results found that sanctuary monkeys did indeed approach faster and spend more time interacting, while in the wild, adult females explored the object the most. Interestingly, both populations used their hands more frequently than their muzzles, potentially due to previous foraging experiments. Notably, there was no significant difference between the populations in exploring with hands vs. muzzle. We hope our project will encourage researchers to test captive and wild animals using touchscreens.

1. Introduction

Throughout their lives, animals have to solve problems critical to their survival, such as foraging, finding mates, and reacting to predators. The main focus of cognitive research is on how animals acquire, use and store information (Shettleworth, 2001). Most studies of animal cognition have been performed in captivity where researchers have easy access to the species and can test them based on individual traits. Automated electronic devices have been used since 1930 to study laboratory animals during simple experiments such as pulling a lever or pressing a button to get a reward (Markowitz, 1982; Skinner, 1988; Washburn & Rumbaugh, 1992). After this first approach, touchscreens, along with radio-frequency identification (Fagot & Paleressompoulle, 2009), facial recognition (McBride et al., 2016), and eye trackers (Krupenye et al., 2016) have been developed and utilised in laboratories and other captive environments. Touchscreen experiments have been employed across a range of species, including rats (*Rattus norvegicus domestica*, Bussey et al., 2008), dogs (*Canis familiaris*, Range et al., 2008), pigeons (*Columba livia domestica*, Stephan et al., 2012), turtles (*Chelonoidis carbonaria*, Mueller-Paul et al., 2014), sheep (*Ovis aries,* McBride et al., 2016*)* and chimpanzees (*Pan troglodytes*, Matsuzawa, 1985). Martin et al. (2022) note that technological innovations have been developed to test animals in their natural environments and therefore decrease the influence of human proximity. According to Hopper (2017), using consistent methodology facilitates the comparison of cognitive abilities across different species in different contexts. In addition, the new devices provide enrichment opportunities in a controlled environment, ultimately improving animal welfare (Webb et al., 2019). While laboratory experiments are convenient, researchers have shown a growing interest in testing animals in their natural habitats (Morand-Ferron et al., 2015). For instance, touchscreen technology has recently been applied in field experiments. Harrison et al. (2023) adapted a touchscreen originally used in a zoo (Schmitt, 2018) for use in a natural setting. Their study found that captive and wild monkeys performed similarly in an associative learning task, despite differences in participation rates. Furthermore, the participation of wild monkeys seemed to be influenced by individual factors such as age and sex, with adult females and juvenile males being the most likely participants. These results align with previous studies that have demonstrated how contextual variables, such as captivity, season, food deprivation can impact participation (Benson Amram et al., 2013; Martina et al., 2021; Morand-Ferron et al., 2015; Thornton & McAuliffe, 2006; van de Waal et al., 2010; van Horik et al., 2017). However, there is an alternative possible explanation for the different levels of participation seen between individuals. Neophobia has been defined as the fear of something new or unfamiliar (Greenberg & Mettke-Hofmann, 2001). Cole and Quinn (2012) found that neophobic great tits (*Parus major*) were less likely to explore novel food sources than less neophobic individuals. Neophobia has been shown to influence fitness (Ferrari & Chivers, 2008), responses to stress (Carere & van Oers, 2004), and the ability to innovate (Greenberg, 2003).

1.1 Influence of individual traits on latency to approach novel objects

Studies suggest that an individual's age can influence their approach to a new object or food. Juvenile animals are typically less fearful and more exploratory than adults (Biondi et al., 2010; Douglas et al., 2003; Fairbanks, 1993), resulting in shorter latencies when approaching novel objects (Bergman & Kitchen, 2009; Miller et al., 2015; O'Hara et al., 2017; Sherratt & Morand-Ferron, 2018). This behaviour is due to their need to learn about their environment and potential resources after their initial period of maternal dependence (Thornton & Clutton-Brock, 2011; van de Waal et al., 2012). Juvenile raptors (*Milvago chimango*) showed a shorter latency to feed and higher success rates in solving novel tasks compared to adults (Biondi et al., 2010). Additionally, juvenile baboons (*Papio ursinus*) and ravens (*Corvus corax*) approached all stimuli with shorter latencies than adults in a novel object test (Martina et al., 2021; Miller et al., 2015). In line with previous studies even, in vervet monkeys, juveniles' latency to approach an unfamiliar and potentially dangerous situation increased as they matured into adulthood (Fairbanks, 1993). This trend aligns with the fact that adults with more experience tend to avoid unfamiliar situations to reduce their risk of harm (Crane et al., 2020). When making decisions, animals should consider the balance between benefits and costs, which can vary between sexes. However, despite the high cost, females may still be driven by physiological needs such as hunger to approach novel objects. In another study on wild vervet monkeys and their participation in a touchscreen experiments, Harrison et al. (2023) observed that adult females were more likely to participate than adult males. Females often face a trade-off between feeding themselves and protecting their offspring, whereas males tend to be bolder and more likely to approach new objects in general (Blaszczyk, 2017; Schuett et al., 2010). For example, in a fake predator experiment, Blaszczyk (2017) found that male vervet monkeys approached both snakes and lizards more frequently than females.

1.2 Factors shaping object exploration

Researchers have found that providing animals with man-made objects, such as rope and cloth, in their enclosures can reduce their stress levels and increase their curiosity towards unfamiliar objects (Paquette & Prescott, 1988). Different animals have their own unique ways to respond to novelty (Forss et al., 2021; Martina et al., 2021; Takola et al., 2021) such as dogs and pigs (*Sus scrofa*) using their sense of smell (Cox et al., 2020; Wood-Gush & Vestergaard, 1991), Goffin's cockatoos (*Cacatua goffiniana)* using their beaks and feet (Rössler et al., 2020), and primates using their hands and muzzle to use tools and solve tasks (Bardo et al., 2017; Rogers, 2018). Despite the similarities in experiments, individual variation in exploration has been inconsistent across different species. Differences in animal behaviour towards novel objects may be influenced by various factors:

The first factor that could impact exploration could be based on the free time hypothesis. The free time hypothesis suggests that animals with less disturbance from predators and daily activities may have more energy and time to explore, as observed in juvenile chimpanzees and orangutans (Forss et al., 2021; Kummer & Goodall, 1985). For example, baboons may be less neophobic due to their adaptable and varied diet, than gelada monkeys (*Theropithecus gelada*), whose diet is more specialist of over 90% grass (Bergman & Kitchen, 2009). The presence of abundant food and water in the enclosures could explain the higher innovative and curious behaviour shown in captivity compared to their wild conspecifics (Kummer & Goodall, 1985). Despite the necessity hypothesis' suggestion that the availability of food in enclosures may not motivate captive animals to explore and discover new resources as frequently as they would in the wild (Grund et al., 2019; P. C. Lee & Antonio, 2015) we hypothesize that the sanctuary monkeys will exhibit more exploratory behaviours towards the touchscreen compared to wild individuals, supporting the free time hypothesis.

The second factor that could influence individual's propensity for approaching new things is social context. Species living in large groups, such as ravens (*Corvus corax*) and tufted capuchins (*Cebus apella*), are typically less intimidated by new experiences when in the company of other group members (Reviews by Galef et al., 1990; Galef Jr & Giraldeau, 2001; Stöwe et al., 2006; Visalberghi et al., 2003). Liker and Bókony (2009) found that house sparrows, (*Passer domesticus)* were more likely to approach unfamiliar food when accompanied by a partner or family member than alone. Additionally, Costa et al. (2014) found that calves (*Bos taurus*) living in social groups were more willing to try new foods compared to solitary calves. When accompanied by other orangutans (*Pongo pygmaeus*), adults and juveniles were more likely to explore novel objects than when alone (Schuppli et al., 2017). Similar results were seen in ravens, who approached new objects more quickly when alone but spent more time interacting with them when with other ravens (*Corvus corax*, Stöwe et al., 2006).

Finally, the third factor potentially impacting neophobia and novel object exploration is age (Reader & Laland, 2001). Researchers have shown that juvenile chimpanzees spend more time interacting with objects, despite having no reason to use them, compared to adults who have more goal-directed choices (Lamon et al., 2018). Similarly, in an experiment with wild orangutans, Schuppli et al. (2021) found that juvenile orangutans explored objects more than adults. In a novel object experiment with human infants, Ruff et al. (1992) discovered that five- and eleven-month-old human infants were more likely to use their mouths than their hands to acquire information. The results were similar in juvenile orangutans, who explored novel objects with their mouths compared to adults who used their hands (Ruff et al., 1992; Schuppli et al., 2021). Furthermore, in a social learning experiment, dog pups used their muzzles rather than their paws to solve a task (Fugazza et al., 2018). This suggests that juvenile animals may use the part of their body that is more developed and precise in accomplishing their goals. Two different feeding techniques found in different life stages of birds and orangutans were due to a lack of precision and slow development (Marchetti & Price, 1989). As they age, immature orangutans not only change their dietary choices, but also become more familiar with using other body parts, such as arms and legs, for daily activities that were previously used to cling to their mother's belly until they reach independence. Although juveniles use both hands and muzzle to acquire information and manipulate objects, they switch to using only their hands as adults (Schuppli et al., 2016). Moreover, following the enculturation hypothesis, the animals' close proximity to the human world may potentially increase their trustworthiness towards any items presented by researchers, including the touchscreen in our study (van Schaik & Burkart, 2011).

1.3 Enculturation hypothesis

The majority of the sanctuary monkeys included in the present study were raised in proximity to humans during their early development. Earlier studies have suggested that the cognitive and tool manipulation behaviour of animals is affected by their upbringing environment (Tomasello et al., 1993; van de Waal, 2010). There are numerous experiments that demonstrate animals' abilities to observe and learn from their social counterparts, as seen in fish (Brown & Laland, 2003), birds (Slagsvold & Wiebe, 2011), and primates (Canteloup et al., 2020; van de Waal et al., 2014). It is clear that social learning is an important skill across a variety of species. Animals that have had extensive interactions with humans or have been exposed to human environments for an extended period are more likely to demonstrate learning from them through imitation (Galef & Heyes, 2004). Most research on enculturated animals has focused on their ability to imitate and perform specific human actions while problem-solving (Tomasello et al., 1993). Our study explores whether there are differences in how animals approach unfamiliar stimuli. Based on the enculturation hypothesis, we predicted a difference in behaviour between sanctuary monkeys and their wild counterparts when interacting for the first time with a touchscreen. We expected sanctuary monkeys to display less vigilance and more direct interactions in comparison to the wild monkeys.

1.4 Aims and hypotheses

The aim of the study was to investigate how age, sex, and context (wild or sanctuary) effects the approach and explorative behaviour of vervet monkeys towards a novel object: the portable touchscreen. Vervet monkeys were chosen for this study because of their easy observability, semi-arboreal nature, and social group living with both males and females. Predictions were made based on previous studies (Harrison et al., 2023) that suggested three variables would influence the duration and latency of animal approach and manipulation time of exploration: sex (female vs. male), age class (adult vs. juvenile), and category (wild vs. sanctuary). It was anticipated that within the wild population, adults would approach the touchscreen faster than juveniles due to food motivation and low risk of danger. Among adults, females, were predicted to interact first and for longer than males. It was hypothesized that sanctuary individuals would approach the touchscreen faster and stay longer compared to their wild counterparts, due to the free time hypothesis. Additionally, we expected that as vervet monkeys aged, the way they explored the touchscreen would change: the number or rate of behaviours performed per minute would increase, and there would be a shift in body parts used during exploration from the mouth to hands during adulthood.

2. Method and material

2.1 Subjects

From August 2019 to February 2021, we conducted the experiment on wild vervets at the Inkawu Vervet Project (IVP) in the Mawana Game Reserve located in KwaZulu-Natal, South Africa, in five groups of wild vervet monkeys (Ankhase: N = 21, Baie Dankie: N = 49, Kubu: N = 19, Lemon tree: N = 24, Noha: N = 32, Table. 1). A team of 10 researchers helped to identify each monkey based on their unique physical features, such as scars, ear notches, and body shape. Ankhase, Baie Dankie, Noha, and Lemon Tree had been habituated to human presence since 2010, while Kubu had been habituated since 2013. Furthermore, from August 2018 to October 2018 data on captive vervets was collected from three groups of sanctuary vervet monkeys (Boeta: N = 3, Liffie: N = 22, Poena: N = 11) at the Wild Animals Trauma Center and Haven (W. A. T. C. H.) in Vryheid, KwaZulu Natal, South Africa. All groups lived in social groups in enclosures and were provided with water and food (vegetables and fruits) once a day. These monkeys were brought to the sanctuary as orphans from various backgrounds, such as rescues from roadsides or the black market, or as injured individuals. Most of them arrived at the sanctuary as orphans when they were just a few weeks old and were bottle-fed by W. A. T. C. H. staff until they were three months old. At that point, they were introduced to one of the group of individuals of mixed ages living in the enclosures. The aim of the sanctuary is to reintroduce these monkeys back into the wild, so human interaction with them has been limited to researchers and staff.

Both wild and sanctuary monkeys were not habituated to using touchscreens and they had not previously been involved in such experiments. Females were designated as adults following their first birth or upon reaching the age of five, whereas males were classified as adults once they left their group or reached five years of age. Juvenile animals were categorized as such from the age of four months, when they became independent from their mother, until they reached adulthood. Infants under the age of four months were not included in the dataset.

Table. 1: Number of individuals that approached the touchscreen at least once during the first exposition in each group.

Context	Date	Group	Age Sex Class	Total number participants	Total number	Average number of approaches
Wild	07.01.2020	Ankhase	Adult Female	2	7	5
			Adult Male	0	2	0
			Juvenile Female	1	5	5
			Juvenile Male	5	6	2.8
	23.02.2021	Baie Dankie	Adult Female	2	19	3
			Adult Male	3	9	5
			Juvenile Female	4	17	4.25
			Juvenile Male	2	19	4
	03.08.2019	Noha	Adult Female	1	12	8
			Adult Male	2	6	1.5

			Juvenile Female	2	4	3
			Juvenile Male	1	8	2
	10.09.2019	Lemontree	Adult Female	2	8	4
			Adult Male	2	3	7
			Juvenile Female	3	7	3
			Juvenile Male	3	6	7.6
	09.11.2019	Kubu	Adult Female	2	4	13
			Adult Male	1	1	8
			Juvenile Female	0	7	0
			Juvenile Male	1	6	10
Sanctuary	31.08.2018	Boeta	Adult Female	1	1	11
			Adult Male	2	2	5.5
			Juvenile Female	0	0	0
			Juvenile Male	0	0	0
	11.09.2018	Liffie	Adult Female	0	1	0
			Adult Male	1	1	27
			Juvenile Female	4	10	13.6
			Juvenile Male	3	11	10
	07.09.2018	Poena	Adult Female	1	1	20
			Adult Male	0	0	0
			Juvenile Female	2	2	10.5
			Juvenile Male	6	8	22

2.2 Ethical statement

Our study adhered to the ASAB/ABS Guidelines for the use of animals in research (2020) and was approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa.

2.3 Material and procedure

We introduced a portable touchscreen (Zoo based-Animal-Computer-Interaction System (ZACI)), to vervet monkeys adapted from a touchscreen originally built for research on primates and birds in zoos (Schmitt, 2018). In the wild, experiments were conducted early in the morning, after sunrise, when the monkeys were still in their sleeping site. Depending on the season, the time the monkeys spent at their sleeping site varied. During the winter seasons, they sunbathed on the top of the canopy, while in the summer, they left early in the morning to start their daily routine. Once the monkeys entered a one-meter area around the touchscreen, the experimental session began. In captivity, the tests were conducted either in the afternoon or early morning to avoid sunlight reflecting off the screen and before feeding the monkeys. The experiment began as soon as the touchscreen was attached to the enclosure with hooks. Sanctuary monkeys were attracted by dropping a few soaked corns into the hole in the touchscreen, where they could access the reward, and spreading soaked corns around the touchscreen. Each experiment was recorded using a JVC EverioR Quad Proof GZ-R415BE camera mounted on a tripod, and the videos were later encoded by TM and SG.

2.4 Video coding and measurements

Throughout the trials, we recorded the start and end times, which began when the first individual approached within one meter and ended when all individuals had left the sleeping site, or after a maximum of 35 minutes for sanctuary groups. To ensure precise video coding, a second coder independently coded three of the five experimental sessions in the wild, with an agreement rate of 0.8 kappa. Additional information on the experiments can be found in Supplementary Data Table. S1. We also recorded the time it took for each individual to approach and interact with the touchscreen during each experiment. A detailed breakdown of the video coding with the latency and duration can be found in Supplementary Material. To monitor the monkeys' exploration behaviour, we utilised an ethogram developed by Forss et al. (2021). We recorded the number of times a monkey sniffed, bit, or tasted the touchscreen (mouth exploration), as well as the number of times they touched the touchscreen, or manipulated it by interacting with the hooks or grabbing the side (hand exploration). These behaviours are documented in Supplementary Material. Furthermore, we classified the social conditions as 'alone' if the subject approached the touchscreen alone or 'with someone' if the individual approached the touchscreen with at least one other group member.

2.5 Statistical analyses

Before running the singular analyses, we ran a Spearman's rank correlation test to test whether there was a correlation between the latency to approach the touchscreen and the interaction time per individual.

We utilised a mixed effects Cox regression model powered by the 'coxme' R package (Therneau & Therneau, 2015), to examine whether context (wild: N = 145 vs. sanctuary: N = 36) effected the time it took for an individual to approach the touchscreen. A Cox regression was an appropriate choice for analysing time to event data (in our case, approaching the touchscreen). Our model produced hazard ratios, where an HR > 1 indicated a positive relationship between a variable and the event, while an HR < 1 indicated a negative relationship. In this instance, an HR > 1 suggested a heightened likelihood of approaching the touchscreen, whereas an HR < 1 indicated the opposite. Additionally, we conducted another Cox regression model to investigate the influence of age class (adult: N = 71; juvenile: N = 85) and sex (males: N = 66; females: N = 90) on the latency to approach the touchscreen. However, we only utilised data from wild groups since the number of individuals in sex and age class was significantly imbalanced between the sanctuary and wild groups. Lastly, we applied the Tukey correction to perform multiple comparisons between the five wild groups.

First, a gamma generalized linear mixed effects model (GLMM1) was run to assess the influence of context (wild: N = 39 vs. sanctuary: N = 21) on touchscreen interaction time. Furthermore, we utilised a second gamma model (GLMM2) to investigate whether the time spent interacting with the touchscreen was affected by the interaction between age class, sex and group.

The study examined how contextual factors, such as the type of exploration (mouth or hands) and social conditions (alone or with someone), impacted the exploratory behaviour of individuals interacting with a touchscreen. Negative binomial distributions were utilised to account for overdispersion, and all 60 participants from the first exposure were included in the analysis, with random effects for individual and group. Two additional negative binomial models were applied to control for overdispersion in the influence of age class and sex and type of exploration, respectively, using only wild groups. Individual was used as a random variable in the last two models.

All three analyses were conducted using R (version 4.2.1, R CoreTeam, 2013) and R Studio (version 2022.07.1+554, RStudio Team, 2020), with an alpha level of 0.05.

3. Results

We found a weak negative correlation between the latency to approach the touchscreen and the time interacting with it (r = - 0.47, p = 0.0001). Our results indicate that individuals who approached the touchscreen more quickly tended to spend more time interacting with it, while those who took longer to approach it spent less time interacting with it.

3.1 Analysis 1: Effect of Context, Age and Sex on individual latency to approach the touchscreen

At the sanctuary the time it took for individuals to approach the touchscreen varied greatly, ranging from mere seconds (3.46 seconds) to several minutes (6.17 minutes), with an average time of just over 53 seconds (53.47 seconds). Meanwhile, in the wild, groups of individuals took anywhere from just over 9 seconds (9.18 seconds) to almost 38 minutes (37.54 minutes) to approach the touchscreen, with an average time of just over 9 minutes (9.62 minutes, Table. S2).

After running a regression model, we found that sanctuary individuals approached the touchscreen significantly quicker than those in the wild (Cox model: HR = 0.270, p < 0.001, Table. 2, Figure. 1).

Table. 2: Results of a Cox mixed effects survival model predicting the latency to approach the touchscreen for each individual from both sanctuary and wild groups.

	Coef	**Exp(coef)**	**se(coef)**	**z**	**p-value**
Context (wild)	-1.3084	0.2703	0.2746	-4.765	1.89e-06

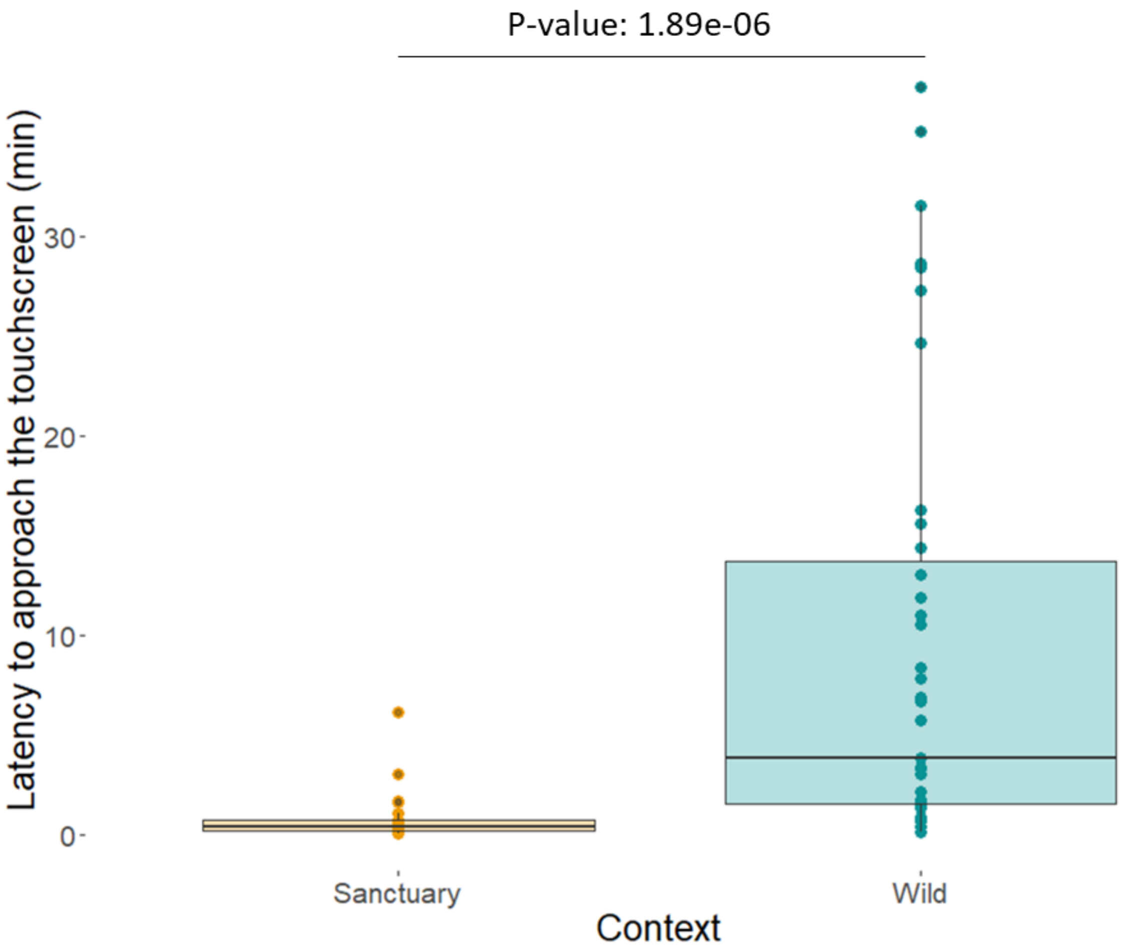


Figure. 1: Boxplot of the distribution of the latency to approach the touchscreen observed in sanctuary (N = 21) and in wild individuals (N = 39). The solid horizontal line shows the median latency to approach the touchscreen. Upper and lower limits of the box show the first and third quartiles, dots represent individuals.

During the analysis, three Cox regression models were utilised to test factors that affect the time it takes individuals to approach a touchscreen. The second model suggested a potential effect of the interaction of sex and age class and the latency to approach (HR = 0.28, p = 0.056). However, the third model was conducted without any interaction, and it showed that sex has a trend impact on latency to approach the touchscreen (HR = 1.87, p = 0.075, Table. 3). Specifically, it seemed that males tend to approach the touchscreen slower than females. Age class, on the other hand, was not found to have a significant effect on latency to approach (HR = 0.86, p = 0.665). Additionally, the Ankhase group (N = 20) approached the touchscreen faster than the Baie Dankie (N = 64, p = 0.029), Noha (N = 30, p = 0.026) and Kubu (N = 18, p = 0.049, Table. S5) groups.

Table. 3: Results of a Cox mixed effects survival model predicting the latency to approach the touchscreen showed by individuals in wild population during first exposition.

Effect	coef	Hazard Ratio	p-value
Age Class (juvenile)	-0.15	0.86	0.665
Sex (male)	0.63	1.87	0.075
Group Baie Dankie	-1.21	0.29	**0.012**
Group Kubu	-1.17	0.31	**0.059**
Group Lemon Tree	-0.36	0.69	0.447
Group Noha	-1.38	0.26	**0.016**

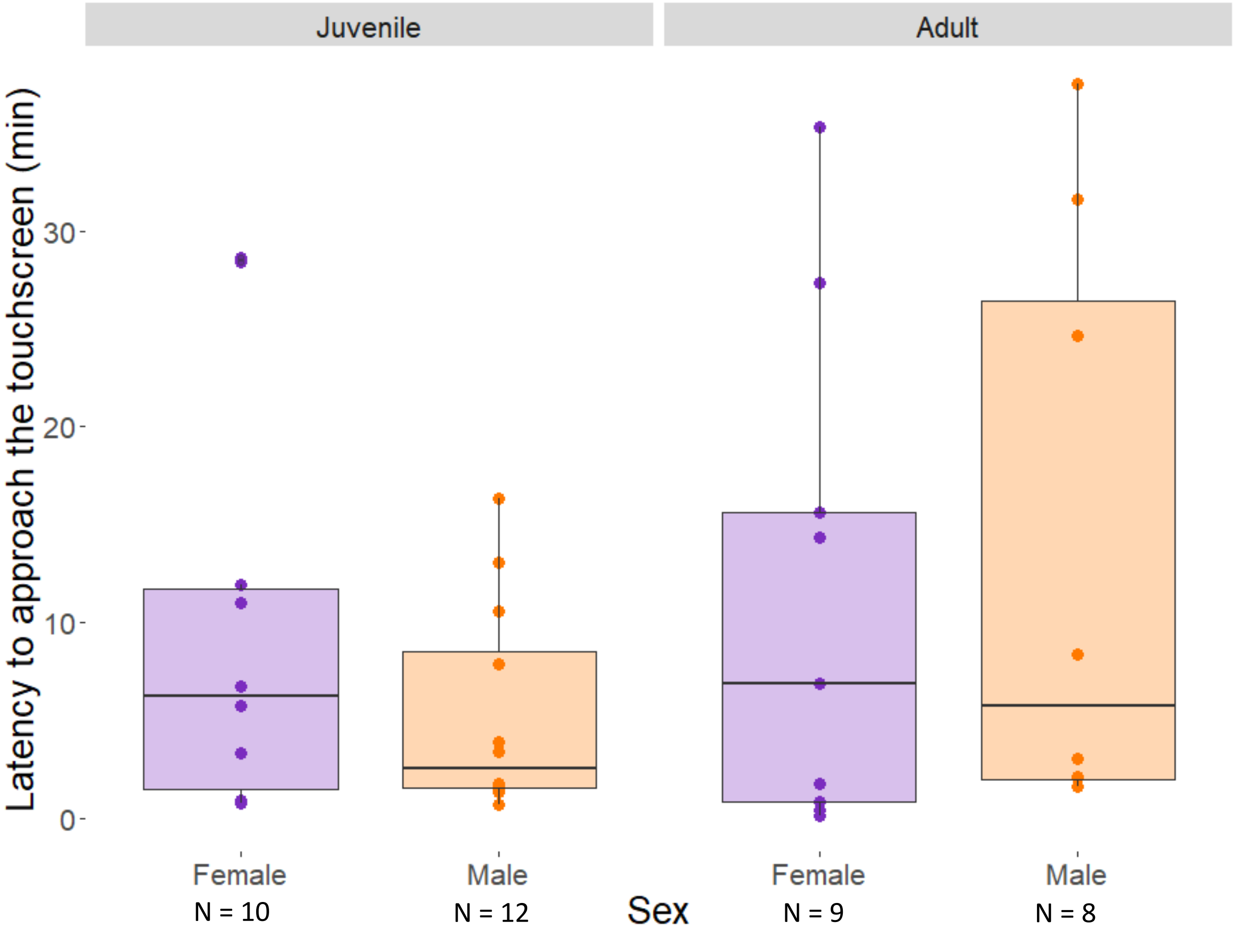


Figure. 2: Boxplot showing the distribution of the latency by age-and sex class, with solid horizontal lines showing the median latency, upper and lower limits of the box showing the first and third quartiles and points representing the latency observed in each individual, coloured by sex.

3.2 Analysis 2: Duration of interaction with the touchscreen between sanctuary and wild groups

The wild monkeys' interaction time ranged from 7.79 seconds to 31.74 minutes, with an average of 6.12 minutes and a standard error of 77.82 seconds. The sanctuary monkeys' interaction time varied from 2.01 minutes to 27.42 minutes, with an average of 9.26 minutes and a standard error of 18.37 seconds. Additional information can be found in Table. S4.

In the first gamma distribution model we did not find any significant difference in time of interaction with the touchscreen between sanctuary and wild groups (β = -0.46, p = 0.183, Figure. 3, Table. 4).

Table. 4: Results of a GLMM predicting the time interacting with the box by sanctuary and wild groups during the first exposition.

N = 10 N = 12 N = 9 N = 18

Effect	**Estimate**	**Std.Error**	**p-Value**
Intercept	2.68	0.32	3.15e-11 ***
Context (wild)	-0.46	0.28	0.183

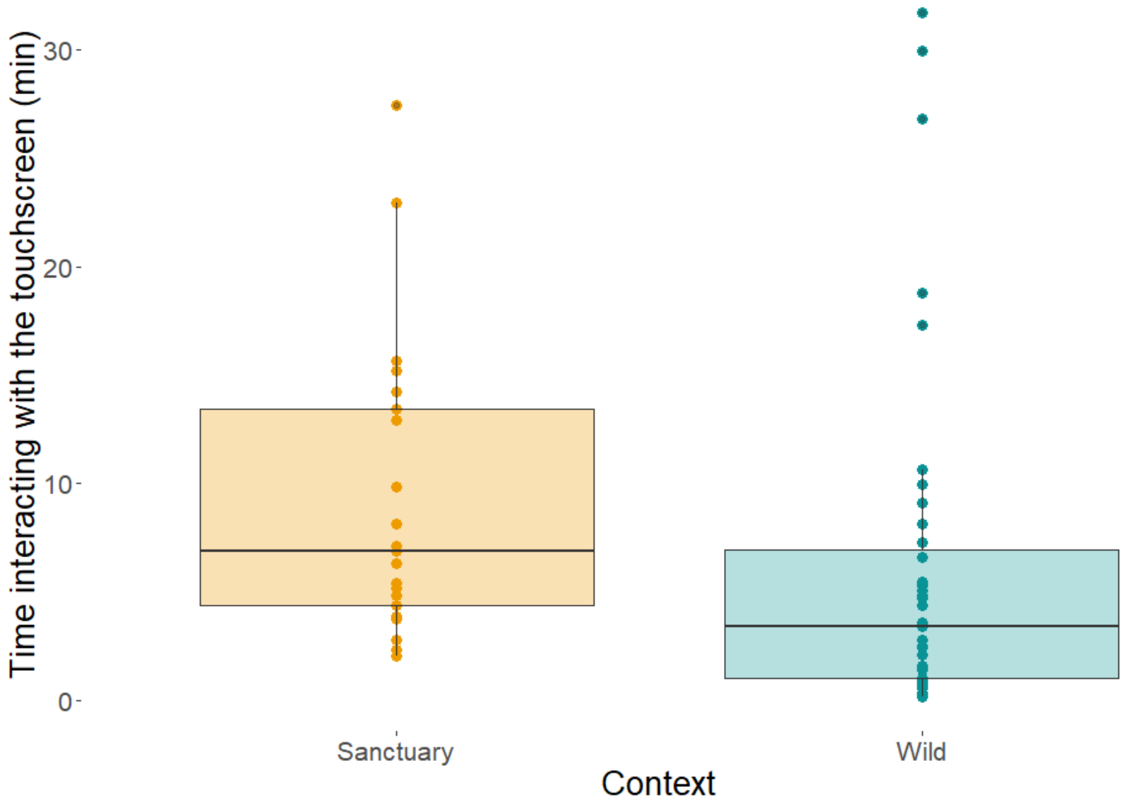


Figure. 3: Boxplot of the distribution of the time interacting with the touchscreen observed in sanctuary (N = 21) and wild individuals (N = 39). Upper and lower limits of the box show the first and third quartiles, dots represent individuals.

The second full gamma mixed model was significantly better than the null model (χ2 = 18.01, p = 0.0048). Although we did not observe a significant interaction between age class and sex (β = 0.82, p = 0.240) within wild groups, we did notice a significant difference in how much time individuals spent interacting with the touchscreen based on their age class. Specifically, juvenile monkeys (N = 22) spent less time than adults (N = 17, β = -0.78, p = 0.024), with no significant variation between sexes (β = -0.03, p = 0.920, as shown in Table. 5). Additionally, we conducted a post-hoc Tukey test, indicating a similar time correlation among the groups, with a possible tendency for Kubu to interact for longer compared to the other groups (Table. S9, Figure. S3).

Table. 5: Results of a GLMM predicting the time interacting with the touchscreen for each individuals between age class, sex and group in wild population only.

Effect	**Estimate**	**Std.Error**	**p-value**
Intercept	1.51	0.46	0.003
Age Class (juvenile)	-0.78	0.33	**0.024**
Sex (male)	-0.03	0.31	0.920
Group Baie Dankie	0.06	0.46	0.900
Group Kubu	1.55	0.62	**0.019**
Group Lemon Tree	0.89	0.47	0.066
Group Noha	0.78	0.54	0.152

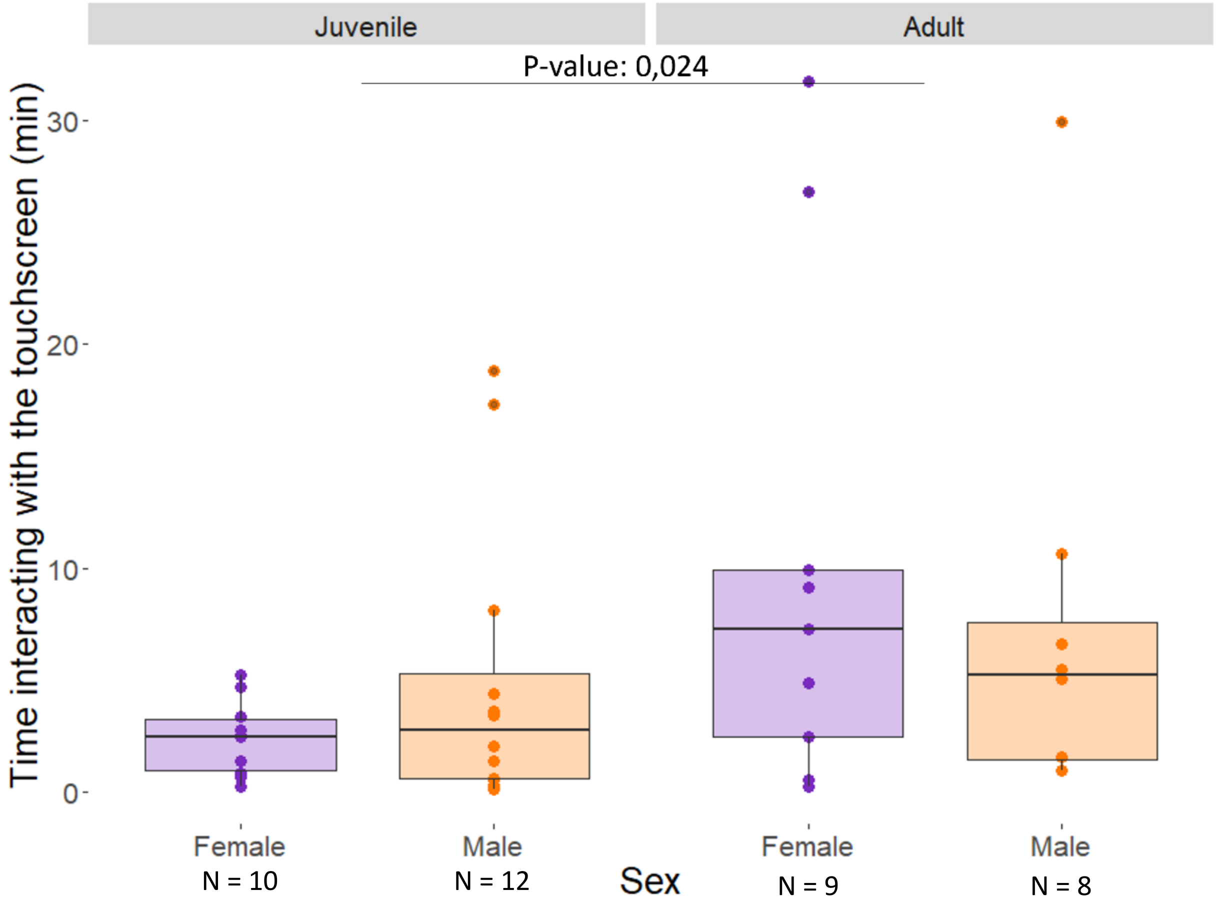


Figure. 4: Boxplot of the distribution of the time interacting with the touchscreen by each age class and sex class, with solid horizontal lines showing the median duration, upper and lower limits of the box showing the first and third quartiles and points representing the duration of each individual, coloured by sex (violet: female, orange: male).

3.3 Analysis 3: Comparison of explorative behaviours displayed by wild and sanctuary monkeys

Our research analysed individual behaviour during the first trial using a negative binomial distribution model. We discovered that this model performed significantly better than the null model ($\chi2 = 42.9$, $p < 0.001$) after excluding non-significant interactions between context and type of exploration ($\beta = 0.26$, $p = 0.428$), as well as type of exploration and social condition ($\beta = 0.43$, $p = 0.174$). While we did not observe a significant effect of context on behaviour rate ($\beta = 0.21$, $p = 0.274$), we did find that the type of exploration ($\beta = -0.40$, $p = 0.011$) and social condition ($\beta = 1.09$, $p < 0.001$, Table. 6) had significant effects. When exploring the touchscreen, both wild and captive monkeys used their hands more than their mouths. In addition, it was intriguing to see that both wild and sanctuary populations exhibited a higher rate behaviours when they were with someone than when they were alone (Figure. 5). See supplementary data for the ethogram description.

Table. 6: Results of a GLMM predicting the rate of behaviours showed using hand and mouth exploration in different social condition between wild and sanctuary groups.

Effect	**Estimate**	**Std. Error**	**p-value**
Intercept	-1.19	0.22	<0.001
Social condition (with someone)	1.09	0.17	**<0.001**
Type of exploration (mouth exploration)	-0.40	0.16	**0.0111**
Context (wild)	0.23	0.21	0.274

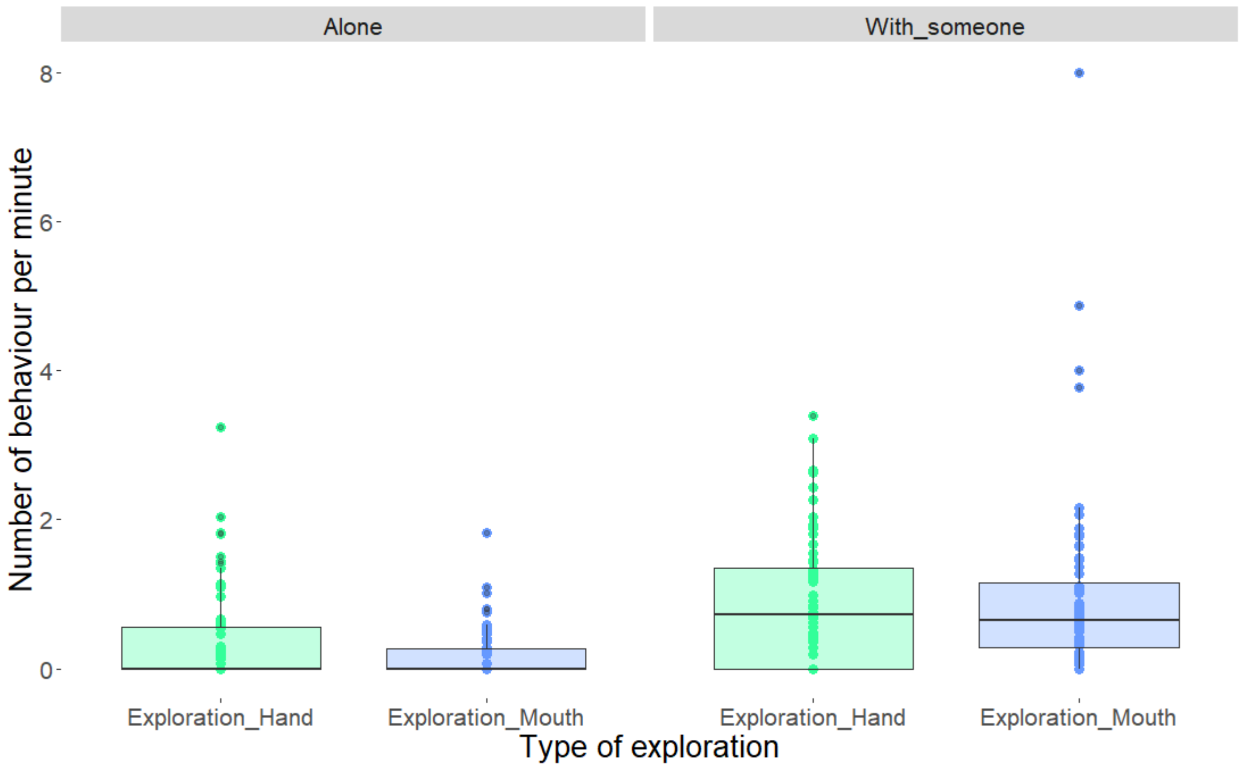


Figure. 5: Boxplot of the distribution of rate of explorative behaviours displayed for each type of exploration: hand (green) and mouth (blue). Solid horizontal lines show the median rate, upper and lower limits of the box show the first and third quartiles and points represents behaviour observed by each individual.

Our study focused on examining the influence of an interaction between age class and sex on exploration rate within wild groups. We conducted a third and fourth negative binomial distribution models to determine if there was an impact on the rate of behaviours resulting from interactions between age class and sex, as well as age class and exploration type. The results showed no significant influence from the interaction between age class and sex (β = -0.55, p = 0.196) or between age class and exploration type (β = 0.64, p = 0.096). We then removed all interactions and conducted a fifth model, which revealed no significant effect of exploration type (β = -0.26, p = 0.249) or age class (β = -0.23, p = 0.300). However, we did detect a noteworthy effect of sex (β = -0.51, p = 0.025, Table. 7). It was noted that wild males exhibited a lower rate of exploratory behaviour than wild females when interacting with the touchscreen (Figure. 6).

Table. 7: Results of a GLMM predicting the rate of behaviours showed between Age Class, Sex in wild population only.

Effect	Estimate	Std.Error	p-value
Intercept	-0.11	0.21	0.584
Type of exploration (mouth exploration)	-0.26	0.20	**0.249**
Age (juvenile)	-0.23	0.22	0.3000
Sex (male)	-0.51	0.23	**0.025**

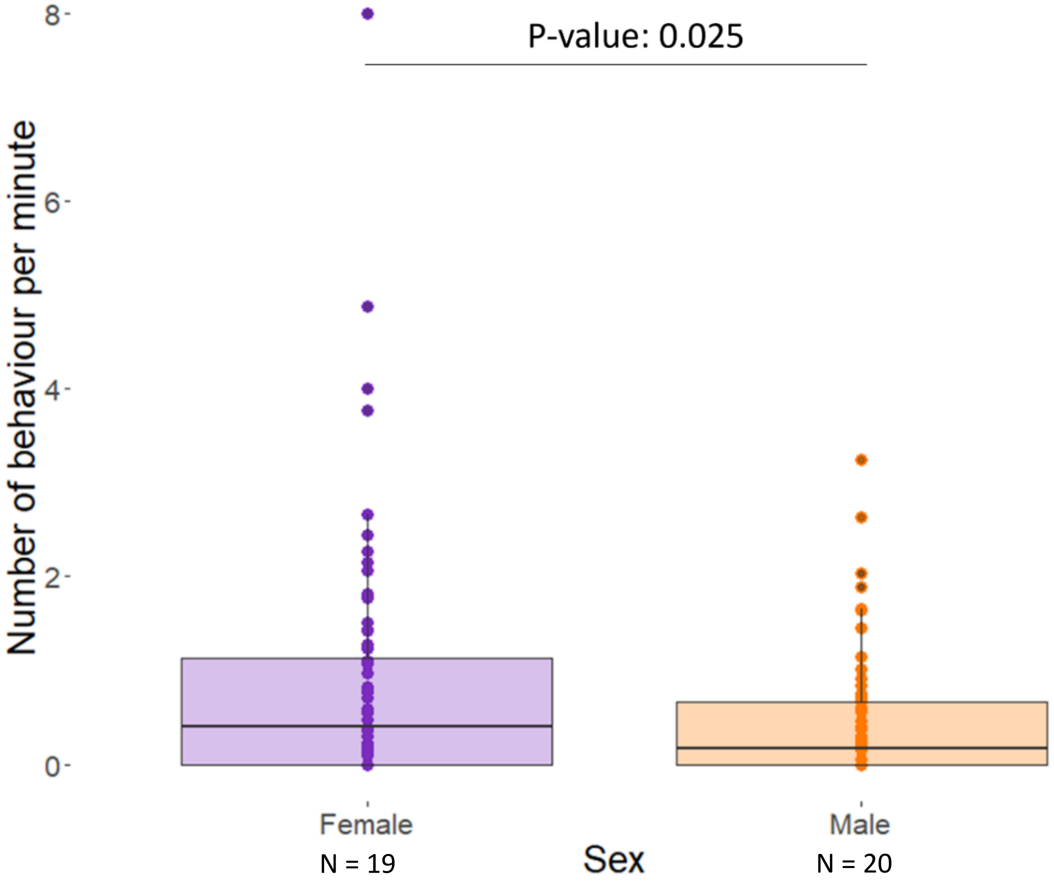


Figure. 6: Boxplot of the distribution of the number of behaviours per minute by each sex class, with solid horizontal lines showing the median time, upper and lower limits of the box showing the first and third quartiles and points representing the number of behaviour per minute observed in each individual.

4. Discussion

4.1 Aim and results

In this study we analysed the behaviour of both wild and sanctuary vervet monkeys when presented with a novel portable touchscreen. The study specifically examined their response time and exploratory behaviour, focusing on three key aspects: 1) the time it took for the monkeys to approach the touchscreen, 2) the duration of their interactions with the touchscreen, and 3) the frequency of exploratory behaviours exhibited using their hands or mouth.

Throughout the touchscreen experiments, an unfamiliar object was introduced to both wild and sanctuary study groups. Soaked corn was strategically placed around the touchscreen to incentivize the monkeys to interact with it. However, we observed that the wild monkeys took longer to approach the setup compared to their sanctuary counterparts. It is important to note that monkeys in both contexts exhibited a considerable amount of variation in their latency towards the object. The results of this study are consistent with previous research indicating that captive individuals tend to exhibit less neophobia than their wild counterparts (Crane & Ferrari, 2017; Schaffer et al., 2021). The sanctuary monkeys in our study were primarily hand-reared in a human house, where they had regular exposure to mobile phones and TV sets. This exposure may explain why they exhibited a lower level of neophobia towards certain human objects (Tomasello & Call, 1994; van De Waal & Bshary, 2010) as compared to their wild counterparts.

4.2 Effect of Context, Age and Sex on individual latency to approach the touchscreen

Based on our observations, it seems that monkeys at the sanctuary tend to display more curiosity and engage more with touchscreens than wild individuals. This could be due to the lack of danger and the repetitive nature of their environment. On the other hand, wild monkeys showed a different pattern of behaviours, with only a small percentage of the group interacting with the touchscreens, mostly being adults. However, the wild monkeys had the opportunity to interact with other objects, such as puzzle boxes (Bono et al., 2018; Canteloup et al., 2020; van de Waal et al., 2015) and novel foods (Dongre et al., 2021; van de Waal et al., 2013). Our latency results confirmed earlier research indicating that Kubu and Lemon tree groups demonstrated lower familiarity with human presence (Forss et al., 2021) and spent comparatively less time interacting than Ankhase, while not differing from Noha and Baie Dankie. One possible explanation for this difference could be the amount of time the monkeys spent in their sleeping areas before beginning their daily activities. From personal observations, it appeared that the Lemon Tree and Kubu groups took longer to leave the sleeping area, providing them with more time to interact with the touchscreen. It would be interesting to gather data on the time taken by the monkeys to leave the sleep site and compare it with their interaction duration in future experiments. Although previous studies have indicated that juvenile vervet monkeys show less neophobia (Bergman & Kitchen, 2009; Biondi et al., 2010; Visalberghi et al., 2003), we found no differences in latency between adults and juveniles in our results. In agonistic interactions between adults and juveniles, juveniles are generally defeated due to their physical weakness. Therefore, we expected them to avoid competition and conflict by not approaching the touchscreen. However, we observed that in two groups, Ankhase and Baie Dankie, the first individual to approach the touchscreen was a juvenile. In Ankhase, the highest-ranking female did not approach the touchscreen, giving other group members access. This allowed a juvenile male, motivated by the presence of corn, to approach first. In Baie Dankie, the juvenile female approached almost simultaneously with her dominant adult sister. In the three other groups (Kubu, Lemontree, and Noha), it was the adult females who approached first. Our vervet monkey population has exhibited co-dominance, and females have been found to outcompete males in some study groups (Hemelrijk et al., 2020). This may explain why females had more opportunities to approach the touchscreen undisturbed by the rest of the group (Hemelrijk et al., 2020; Harrison et al., 2023)

4.3 Duration of interaction with the touchscreen between wild and sanctuary groups

In accordance with the free-time hypothesis (Kummer & Goodall, 1985), an initial exploration study was conducted to determine if wild and sanctuary vervet monkeys differed in the amount of time spent interacting with a touchscreen. However, our results did not support this hypothesis. We found no discernible difference in interaction time between wild and sanctuary monkeys. Surprisingly, sanctuary monkeys interacted with the touchscreen for similar durations as their wild counterparts, despite being free from predators and having access to food and water in their enclosures. During the dry season when resources were scarce, wild vervets may have been particularly motivated by the food reward, which could have led to increased interaction with it.. Our second hypothesis, which suggested that the level of habituation (Forss et al., 2021) could account for the difference in interaction time between the two contexts. Both wild and sanctuary vervet monkeys interacted with the touchscreens with ease and exhibited exploratory behaviours such as touching and manipulation, even on their first encounter with the touchscreen.

Our research suggests that differences exist in the amount of time individuals from different age groups spend interacting with touchscreens. Specifically, we observed that adults spent more time than juveniles, which differs from previous studies on raptors, wild great tits and hyenas (Benson Amram et al., 2013; Miller et al., 2015; Morand-Ferron et al., 2015). Additionally, females tended to monopolize the touchscreen more often than males. In future studies, it would be interesting to explore the persistence levels of dominant and subordinate individuals, as well as the number of attempts made by each individual to approach the touchscreen. To eliminate the influence of social learning, we only considered the first touchscreen exposure for each group. Consequently, some individuals were not included in our analysis because they were not present or did not approach on the first day but did approach in subsequent trials. It is possible that habituation increased over time, resulting in increased interaction with the touchscreen by individuals.

4.4 Comparison of explorative behaviours displayed by wild and sanctuary monkeys

When animals encounter a new object, they tend to interact with it in two stages. The first stage is instinctual, where the animal quickly interacts with the object to gather information. The second stage is a habituation stage, where the animal feels more comfortable exploring the object (Takola et al., 2021). For daily activities like grooming and foraging, vervet monkeys use both their hands and mouths. Their mouths are particularly important for olfaction and taste, which helps them collect information about food. Our project aimed to study the different types of exploration between wild and sanctuary monkeys based on the enculturation theory. This theory proposes that animals that live in close proximity to humans are more inclined to trust human objects (van Schaik & Burkart, 2011). Consequently, they may be more likely to use their hands. However, our hypothesis was not supported by our findings. Both groups of monkeys seemed to skip the instinctual stage and move straight to the exploratory stage of touching and manipulating the object. Our analysis only took into account the total number of exploratory behaviours using the mouth and hands. However, it is possible that vervet monkeys use both their hands and mouth from infancy to gather information. In the future, it would be interesting to study the exposure to touchscreens and how individuals choose to explore objects.

During the experiment, it was observed that 26 wild and nine sanctuary monkeys used their sense of smell to approach the touchscreen. Out of these, only 11 monkeys continued to explore the touchscreen using their mouths while the rest used manual exploration. Interestingly, none of the sanctuary monkeys used oral exploration, possibly due to the vervet monkey's tendency to not use their mouth for non-food items. The monkeys interacted with the touchscreen away from the food area, indicating that oral exploration was not necessary for gathering information. Further research could explore if increased exposure and familiarity with touchscreens would lead to all individuals using their hands. Previous studies have indicated that hand preference in primates is linked to brain lateralisation, with wild chimpanzees displaying a greater preference for their right hand for tool use but can switch to their left if necessary to solve a problem (Rogers, 2009). However, juveniles displayed a greater tendency towards mouth exploration, with a possible trend of preference switching from juvenile to adulthood. Investigating when brain lateralisation occurs in the animal's behaviour causing a shift from mouth to hand use would be a valuable avenue for future research.

Our research indicates that, in the wild, female subjects displayed a higher rate of exploratory behaviour, despite the fact that males typically have a greater biological need for exploration, particularly during dispersal. Among adult subjects, females exhibited the greatest level of touchscreen participation, resulting in increased interaction and a broader range of behaviours. Interestingly, we observed that subjects were less likely to explore the touchscreen when they were alone but showed a higher level of risk-taking and interaction when in the presence of others. This aligns with the social facilitation theory that individuals feel less stressed in group settings and are more likely to engage with new objects (Bergman & Kitchen, 2009; Greenberg, 1990). While social facilitation theory suggests that animals perform better in the presence of other group members (Zajonc, 1965), we did not conduct a cognitive task to confirm this. Further research could provide greater insights into this topic.

5. Conclusion

The research explored the initial interactions of vervet monkeys with touchscreens, rather than their problem-solving skills. The study tested both wild and sanctuary populations, which had no prior experience with touchscreens. The results supported the habituation theory, as wild groups took longer to approach the touchscreen than sanctuary groups. Despite the fact that sanctuary individuals had more free time, both populations spent the same amount of time interacting with the touchscreen. Age groups demonstrated a discrepancy in interaction time, with adults spending more time than juveniles. Among adults, females dominated the interaction time and explored the touchscreen with a higher rate of behaviours. Exploration was classified into oral and manual categories, and both populations used their hands more than their mouths to explore the touchscreen. Unfortunately, we did not analyse the choice of body part used for exploration after the first exposure, but it is a topic that could be investigated in future studies. The project underscores the differences and similarities between wild and sanctuary populations and encourages more direct experiments in natural settings. The use of a touchscreen aims to improve comparability between wild and captive experiments and gain a better understanding of animal cognitive abilities.

Acknowledgements

This study was supported by the Swiss National Science Foundation (PP03P3_170624 and PP00P3_198913) and the Branco Weiss Fellowship—Society in Science granted to Erica van de Waal. We are grateful to the van der Walt family for permission to conduct the study at Mawana game reserve and to Sandy Cronk, owner of the rehabilitation centre for permission to conduct the study at W. A. T. C. H. We thank Ezemvelo KZN Wildlife who gave us permission to conduct our research on vervet monkeys in South Africa. We are also grateful to M. Henshall for managing the Inkawu Vervet Project and his help in the data collection. We thank all the team from the IVP for their support and help in data collection. We are grateful to V. Schmitt for her help with the touchscreen procedure and for her participation in the design of the study. Finally, we are grateful to S. Groffi to help with the coding of the videos.

References

Agrillo, C., & Dadda, M. (2007). Discrimination of the larger shoal in the poeciliid fish Girardinus falcatus. *Ethology Ecology & Evolution, 19*(2), 145-157.

Aguzzi, J., Sbragaglia, V., Sarriá, D., García, J. A., Costa, C., del Río, J., Sardà, F. (2011). A new laboratory radio frequency identification (RFID) system for behavioural tracking of marine organisms. *Sensors, 11*(10), 9532-9548.

Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. *Animal behaviour, 38*(3), 486-495.

Bardo, A., Cornette, R., Borel, A., & Pouydebat, E. (2017). Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology, 164*(4), 821-836.

Beach, F. A. (1950). The snark was a boojum. *American Psychologist, 5*(4), 115.

Benson Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta. *Animal behaviour, 85*(2), 349-356.

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (Papio ursinus) and geladas (Theropithecus gelada). *Animal cognition, 12*(1), 63-73.

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal cognition, 13*(5), 701-710.

Blaszczyk, M. B. (2017). Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal behaviour, 123*, 91-100.

Bono, A. E., Whiten, A., van Schaik, C., Krützen, M., Eichenberger, F., Schnider, A., & van de Waal, E. (2018). Payoff-and sex-biased social learning interact in a wild primate population. *Current Biology, 28*(17), 2800-2805. e2804.

Bonter, D. N., & Bridge, E. S. (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology, 82*(1), 1-10.

Borgeaud, C., & Bshary, R. (2018). Testing for anticipation of partners' reciprocity and other social parameters: An experimental approach in wild vervet monkeys (Chlorocebus pygerythrus). *Journal of Comparative Psychology, 132*(4), 464.

Brown, C., & Laland, K. N. (2003). Social learning in fishes: a review. *Fish and fisheries, 4*(3), 280-288.

Buchanan, K., & Perera, T. d. (2020). CC-A., & 2012, U.(2020). Guidelines for the treatment of animals in behavioural research and teaching. *Animal behaviour, 159*.

Bussey, T. J., Padain, T. L., Skillings, E. A., Winters, B. D., Morton, A. J., & Saksida, L. M. (2008). The touchscreen cognitive testing method for rodents: how to get the best out of your rat. *Learning & memory, 15*(7), 516-523.

Call, J. E., Burghardt, G. M., Pepperberg, I. M., Snowdon, C. T., & Zentall, T. E. (2017). *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior, Vol. 1*: American Psychological Association.

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. *Nature communications, 11*(1), 1-10.

Canteloup, C., Puga-Gonzalez, I., Sueur, C., & van de Waal, E. (2021). The consistency of individual centrality across time and networks in wild vervet monkeys. *American Journal of Primatology, 83*(2), e23232.

Carere, C., & van Oers, K. (2004). Shy and bold great tits (Parus major): body temperature and breath rate in response to handling stress. *Physiology & behavior, 82*(5), 905-912.

Cauchoix, M., Hermer, E., Chaine, A., & Morand-Ferron, J. (2017). Cognition in the field: comparison of reversal learning performance in captive and wild passerines. *Scientific reports, 7*(1), 1-10.

Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal behaviour, 28*(2), 362-367.

Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *The American Naturalist, 122*(3), 392-412.

Cilulko, J., Janiszewski, P., Bogdaszewski, M., & Szczygielska, E. (2013). Infrared thermal imaging in studies of wild animals. *European Journal of Wildlife Research, 59*, 17-23.

Clark, F. E., Gray, S. I., Bennett, P., Mason, L. J., & Burgess, K. V. (2019). High-tech and tactile: Cognitive enrichment for zoo-housed gorillas. *Frontiers in psychology, 10*, 1574.

Cole, E. F., Morand-Ferron, J., Hinks, A. E., & Quinn, J. L. (2012). Cognitive ability influences reproductive life history variation in the wild. *Current Biology, 22*(19), 1808-1812.

Cole, E. F., & Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences, 279*(1731), 1168-1175.

Cook, R. G. (1993). The experimental analysis of cognition in animals. *Psychological Science, 4*(3), 174-178.

Cook, R. G., Geller, A. I., Zhang, G.-R., & Gowda, R. (2004). Touchscreen-enhanced visual learning in rats. *Behavior Research Methods, Instruments, & Computers, 36*(1), 101-106.

Costa, J., Daros, R., Von Keyserlingk, M., & Weary, D. (2014). Complex social housing reduces food neophobia in dairy calves. *Journal of Dairy Science, 97*(12), 7804-7810.

Cox, E., Mancini, C., & Ruge, L. (2020). *Understanding Dogs' Engagement with Interactive Games: Interaction Style, Behaviour and Personality.* Paper presented at the Proceedings of the Seventh International Conference on Animal-Computer Interaction.

Crane, A. L., Brown, G. E., Chivers, D. P., & Ferrari, M. C. (2020). An ecological framework of neophobia: from cells to organisms to populations. *Biological reviews, 95*(1), 218-231.

Crane, A. L., & Ferrari, M. C. (2017). Patterns of predator neophobia: a meta-analytic review. *Proceedings of the Royal Society B: Biological Sciences, 284*(1861), 20170583.

Cronin, K. A., Bethell, E. J., Jacobson, S. L., Egelkamp, C., Hopper, L. M., & Ross, S. R. (2018). Evaluating mood changes in response to anthropogenic noise with a response-slowing task in three species of zoo-housed primates. *Animal Behavior & Cognition, 5*(2), 209-221.

Cunha, J. M., & Renguette, C. C. (2022). *A Framework for Training Animals to Use Touchscreen Devices for Discrimination Tasks.* Paper presented at the Proceedings of the Ninth International Conference on Animal-Computer Interaction.

Dale, R., Palma-Jacinto, S., Marshall-Pescini, S., & Range, F. (2019). Wolves, but not dogs, are prosocial in a touch screen task. *PloS one, 14*(5), e0215444.

De Waal, F. B., & Tyack, P. L. (2009). *Animal social complexity: intelligence, culture, and individualized societies*: Harvard University Press.

Delfour, F., & Marten, K. (2006). Lateralized visual behavior in bottlenose dolphins (Tursiops truncatus) performing audio–visual tasks: The right visual field advantage. *Behavioural processes, 71*(1), 41-50.

Dongre, P., Canteloup, C., Lanté, G., Cantat, M., & van de Waal, E. (2021). *Role of immigrant males and muzzle contacts in the uptake of a novel food by wild vervet monkeys.* (PhD).

Douglas, L. A., Varlinskaya, E. I., & Spear, L. P. (2003). Novel-object place conditioning in adolescent and adult male and female rats: effects of social isolation. *Physiology & behavior, 80*(2-3), 317-325.

Dumont, J. R., Salewski, R., & Beraldo, F. (2021). Critical mass: The rise of a touchscreen technology community for rodent cognitive testing. *Genes, Brain and Behavior, 20*(1), e12650.

Dunbar, R. I. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 6*(5), 178-190.

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology, 38*(2), 220-235.

Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior research methods, 41*(2), 396-404.

Fairbanks, L. A. (1993). Risk-taking by juvenile vervet monkeys. *Behaviour, 124*(1-2), 57-72.

Ferrari, M. C., & Chivers, D. P. (2008). Cultural learning of predator recognition in mixed-species assemblages of frogs: the effect of tutor-to-observer ratio. *Animal behaviour, 75*(6), 1921-1925.

Forss, Motes-Rodrigo, A., Dongre, P., Mohr, T., & van de Waal, E. (2021). Captivity and habituation to humans raise curiosity in vervet monkeys. *Animal cognition*, 1-12.

Fugazza, C., Moesta, A., Pogány, Á., & Miklósi, Á. (2018). Social learning from conspecifics and humans in dog puppies. *Scientific reports, 8*(1), 1-10.

Galef, B. G., McQUOID, L. M., & Whiskin, E. E. (1990). Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. *Animal Learning & Behavior, 18*(2), 199-205.

Galef Jr, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal behaviour, 61*(1), 3-15.

Galef Jr, B. G., & Heyes, C. (2004). Social learning and imitation. *Learning and Behavior, 32*(1).

García, M. G., Farine, D. R., Brachotte, C., Borgeaud, C., & Bshary, R. (2021). Wild female vervet monkeys change grooming patterns and partners when freed from feeding constraints. *Animal behaviour, 181*, 117-136.

Gazes, R. P., Brown, E. K., Basile, B. M., & Hampton, R. R. (2013). Automated cognitive testing of monkeys in social groups yields results comparable to individual laboratory-based testing. *Animal cognition, 16*, 445-458.

Gower, E. (1992). Short-term memory for the temporal order of events in monkeys. *Behavioural brain research, 52*(1), 99-103.

Greenberg. (1990). Ecological plasticity, neophobia, and resource use in birds. *Studies in Avian Biology*.

Greenberg. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. *Animal innovation*.

Greenberg, & Mettke-Hofmann. (2001). Ecological aspects of neophobia and neophilia in birds. *Current ornithology*, 119-178.

Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates opportunities for chimpanzee tool use. *Behavioral Ecology, 30*(4), 1136-1144.

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal behaviour, 83*(3), 573-585.

Haslam, M. (2013). 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1630), 20120421.

Hemelrijk, C. K., Wubs, M., Gort, G., Botting, J., & van de Waal, E. (2020). Dynamics of intersexual dominance and adult sex-ratio in wild vervet monkeys. *Frontiers in psychology, 11*, 839.

Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: why there is no theory in comparative psychology. *Psychological Review, 76*(4), 337.

Hopper, L. M. (2017). Cognitive research in zoos. *Current Opinion in Behavioral Sciences, 16*, 100-110.

Hopper, L. M., Allritz, M., Egelkamp, C. L., Huskisson, S. M., Jacobson, S. L., Leinwand, J. G., & Ross, S. R. (2021). A comparative perspective on three primate species' responses to a pictorial emotional stroop task. *Animals, 11*(3), 588.

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal cognition, 17*(4), 835-847.

Horn, L., Cimarelli, G., Boucherie, P. H., Šlipogor, V., & Bugnyar, T. (2022). Beyond the dichotomy between field and lab—the importance of studying cognition in context. *Current Opinion in Behavioral Sciences, 46*, 101172.

Huskisson, S. M., Ross, S. R., & Hopper, L. M. (2021). Do zoo visitors induce attentional bias effects in primates completing cognitive tasks? *Animal cognition, 24*(3), 645-653.

Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence: The step from prosimian to monkey intelligence probably took place in a social context. *Science, 153*(3735), 501-506.

Kays, R., Tilak, S., Kranstauber, B., Jansen, P. A., Carbone, C., Rowcliffe, M. J., He, Z. (2010). Monitoring wild animal communities with arrays of motion sensitive camera traps. *arXiv preprint arXiv:1009.5718*.

Kozuch, A. E., & McPhee, M. E. (2014). Effects of environmental complexity and temporary captivity on foraging behavior of wild-caught meadow voles. *Journal of Applied Animal Welfare Science, 17*(2), 157-171.

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science, 354*(6308), 110-114.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 308*(1135), 203-214.

Lamon, N., Neumann, C., & Zuberbühler, K. (2018). Development of object manipulation in wild chimpanzees. *Animal behaviour, 135*, 121-130.

Lee, P. C., & Antonio, C. d. A. (2015). Necessity, unpredictability and opportunity: An exploration of ecological and social drivers of behavioral innovation. In *Animal creativity and innovation* (pp. 317-333): Elsevier.

Leighty, K. A., Maloney, M. A., Kuhar, C. W., Phillips, R. S., Wild, J. M., Chaplin, M. S., & Betting, T. L. (2011). Use of a touchscreen-mediated testing system with mandrill monkeys. *International Journal of Comparative Psychology, 24*(1).

Leinwand, J. G., Huskisson, S. M., Egelkamp, C. L., & Hopper, L. M. (2020). Within-and between-species variation in the responses of three primate species to a touchscreen gambling task. *Learning and motivation, 71*, 101635.

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

Lopresti-Goodman, S. M., & Villatoro-Sorto, B. (2023). The Benefits and Challenges of Conducting Primate Research in Different Settings. *Animals, 13*(1), 133.

MacDonald, S. E., & Ritvo, S. (2016). Comparative Cognition Outside the Laboratory. *Comparative Cognition & Behavior Reviews, 11*.

Marchetti, K., & Price, T. (1989). Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological reviews, 64*(1), 51-70.

Markowitz, H. (1982). *Behavioral enrichment in the zoo*: van Nostrand Reinhold.

Martin, C. F., Muramatsu, A., & Matsuzawa, T. (2022). Apex and ApeTouch: Development of a Portable Touchscreen System and Software for Primates at Zoos. *Animals, 12*(13), 1660.

Martina, C., Cowlishaw, G., & Carter, A. J. (2021). Individual differences in task participation in wild chacma baboons. *Animal behaviour, 172*, 73-91.

Matsubara, S., Deeming, D. C., & Wilkinson, A. (2017). Cold-blooded cognition: new directions in reptile cognition. *Current Opinion in Behavioral Sciences, 16*, 126-130.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature, 315*(6014), 57-59.

McBride, S. D., Perentos, N., & Morton, A. J. (2016). A mobile, high-throughput semi-automated system for testing cognition in large non-primate animal models of Huntington disease. *Journal of neuroscience methods, 265*, 25-33.

McCune, K. B., Jablonski, P., Lee, S.-i., & Ha, R. R. (2019). Captive jays exhibit reduced problem-solving performance compared to wild conspecifics. *Royal Society open science, 6*(1), 181311.

Mertz, J., Surreault, A., van de Waal, E., & Botting, J. (2019). Primates are living links to our past: The contribution of comparative studies with wild vervet monkeys to the field of social cognition. *Cortex, 118*, 65-81.

Miller, R., Bugnyar, T., Pölzl, K., & Schwab, C. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology, 69*(7), 1209-1220.

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

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: associative learning in wild great tits. *PloS one, 10*(8), e0133821.

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological reviews, 91*(2), 367-389.

Morrison, S. K., & Brown, M. F. (1990). The touch screen system in the pigeon laboratory: An initial evaluation of its utility. *Behavior Research Methods, Instruments, & Computers, 22*(2), 123-126.

Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*: South African National Biodiversity Institute.

Mueller-Paul, J., Wilkinson, A., Aust, U., Steurer, M., Hall, G., & Huber, L. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (Chelonoidis carbonaria). *Behavioural processes, 106*, 187-192.

O'Hara, M., Mioduszewska, B., von Bayern, A., Auersperg, A., Bugnyar, T., Wilkinson, A., Gajdon, G. K. (2017). The temporal dependence of exploration on neotic style in birds. *Scientific reports, 7*(1), 1-9.

Paquette, D., & Prescott, J. (1988). Use of novel objects to enhance environments of captive chimpanzees. *Zoo Biology, 7*(1), 15-23.

Pavlov, I. P., & Thompson, W. (1902). The work of the digestive glands: lectures by Professor JP Pawlow.

Perdue, B. M. (2016). The effect of computerized testing on sun bear behavior and enrichment preferences. *Behavioral Sciences, 6*(4), 19.

Pokorny, J. J., & de Waal, F. B. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences, 106*(51), 21539-21543.

Rachel, H., Tecla, M., & Erica, V. d. W. (2023). Lab cognition going wild: Implementing a new portable touchscreen system in vervet monkeys. *Animal Ecology*.

Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of natural stimuli by domestic dogs. *Animal cognition, 11*, 339-347.

Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology, 22*, 787-805.

Roberts, W. A. (2019). The role of context in animal memory. *Learning & Behavior, 47*, 117-130.

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1519), 943-954.

Rogers, L. J. (2018). Manual bias, behavior, and cognition in common marmosets and other primates. *Progress in Brain Research, 238*, 91-113.

Roma, P. G., Silberberg, A., Huntsberry, M. E., Christensen, C. J., Ruggiero, A. M., & Suomi, S. J. (2007). Mark Tests for mirror self-recognition in capuchin monkeys (Cebus apella) trained to touch marks. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 69*(9), 989-1000.

Rössler, T., Mioduszewska, B., O'Hara, M., Huber, L., Prawiradilaga, D. M., & Auersperg, A. M. (2020). Using an Innovation Arena to compare wild-caught and laboratory Goffin's cockatoos. *Scientific reports, 10*(1), 1-12.

Rowell, M. K., Pillay, N., & Rymer, T. L. (2021). Problem solving in animals: proposal for an ontogenetic perspective. *Animals, 11*(3), 866.

Ruff, H. A., Saltarelli, L. M., Capozzoli, M., & Dubiner, K. (1992). The differentiation of activity in infants' exploration of objects. *Developmental psychology, 28*(5), 851.

Schaffer, A., Caicoya, A. L., Colell, M., Holland, R., von Fersen, L., Widdig, A., & Amici, F. (2021). Neophobia in 10 ungulate species—a comparative approach. *Behavioral Ecology and Sociobiology, 75*(7), 102.

Schmitt, V. (2018). Implementing new portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. *bioRxiv*, 316042.

Schmitt, V., Federspiel, I., Eckert, J., Keupp, S., Tschernek, L., Faraut, L., . . . Bugnyar, T. (2016). Do monkeys compare themselves to others? *Animal cognition, 19*(2), 417-428.

Schuett, W., Tregenza, T., & Dall, S. R. (2010). Sexual selection and animal personality. *Biological reviews, 85*(2), 217-246.

Schuppli, C., Forss, S., Meulman, E., Atmoko, S. U., van Noordwijk, M., & van Schaik, C. (2017). The effects of sociability on exploratory tendency and innovation repertoires in wild Sumatran and Bornean orangutans. *Scientific reports, 7*(1), 1-12.

Schuppli, C., Forss, S. I., Meulman, E. J., Zweifel, N., Lee, K. C., Rukmana, E., van Schaik, C. P. (2016). Development of foraging skills in two orangutan populations: needing to learn or needing to grow? *Frontiers in zoology, 13*, 1-17.

Schuppli, C., van Cauwenberghe, A., Setia, T. M., & Haun, D. (2021). The ontogeny of exploratory object manipulation behaviour in wild orangutans. *Evolutionary Human Sciences, 3*.

Sherratt, T. N., & Morand-Ferron, J. (2018). The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal behaviour, 138*, 59-67.

Shettleworth, S. J. (2000). Modularity and the evolution of cognition. *The evolution of cognition, ed. CM Heyes & L. Huber*, 43-60.

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal behaviour, 61*(2), 277-286.

Shettleworth, S. J. (2009). *Cognition, evolution, and behavior*: Oxford university press.

Skinner, B. F. (1988). Preface to the behavior of organisms. *Journal of the Experimental Analysis of Behavior, 50*(2), 355.

Slagsvold, T., & Wiebe, K. L. (2011). Social learning in birds and its role in shaping a foraging niche. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 969-977.

Stephan, C., Wilkinson, A., & Huber, L. (2012). Have we met before? Pigeons recognise familiar human faces. *Avian Biology Research, 5*(2), 75-80.

Steurer, M. M., Aust, U., & Huber, L. (2012). The Vienna comparative cognition technology (VCCT): an innovative operant conditioning system for various species and experimental procedures. *Behavior research methods, 44*, 909-918.

Stöwe, M., Bugnyar, T., Heinrich, B., & Kotrschal, K. (2006). Effects of group size on approach to novel objects in ravens (Corvus corax). *Ethology, 112*(11), 1079-1088.

Takola, E., Krause, E. T., Müller, C., & Schielzeth, H. (2021). Novelty at second glance: a critical appraisal of the novel object paradigm based on meta-analysis. *Animal behaviour, 180*, 123-142.

Team, R. C. (2013). R: A language and environment for statistical computing.

Therneau, T. M., & Therneau, M. T. M. (2015). Package ‘coxme’. *R package version, 2*(5).

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 978-987.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science, 313*(5784), 227-229.

Tomasello, M., Savage-Rumbaugh, S., & Kruger, A. C. (1993). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child development, 64*(6), 1688-1705.

Tomasello, M., & Call, J. (1994). Social cognition of monkeys and apes. *American Journal of Physical Anthropology, 37*(S19), 273-305.

Troje, N. F., & Bülthoff, H. H. (1998). How is bilateral symmetry of human faces used for recognition of novel views? *Vision Research, 38*(1), 79-89.

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate’s foraging decisions. *Science, 340*(6131), 483-485.

van De Waal, E., & Bshary, R. (2010). Contact with human facilities appears to enhance technical skills in wild vervet monkeys (Chlorocebus aethiops). *Folia Primatologica, 81*(5), 282-291.

van de Waal, E., Claidière, N., & Whiten, A. (2013). Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. *Animal behaviour, 85*(1), 71-76.

van de Waal, E., Claidière, N., & Whiten, A. (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. *Animal cognition, 18*(3), 617-627.

van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matrilines in wild vervet monkeys. *PloS one, 7*(4), e35694.

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society of London B: Biological Sciences, 277*(1691), 2105-2111.

van de Waal, E., & Whiten, A. (2012). Spontaneous emergence, imitation and spread of alternative foraging techniques among groups of vervet monkeys.

van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal behaviour, 90*, 41-45.

van Horik, J. O., Langley, E. J., Whiteside, M. A., & Madden, J. R. (2017). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural processes, 134*, 22-30.

Visalberghi, E., Janson, C., & Agostini, I. (2003). Response toward novel foods and novel objects in wild Cebus apella. *International Journal of Primatology, 24*(3), 653-675.

Vonk, J. (2016). Advances in animal cognition. In (Vol. 6, pp. 27): MDPI.

Vonk, J., & Beran, M. J. (2012). Bears ‘count’too: quantity estimation and comparison in black bears, Ursus americanus. *Animal behaviour, 84*(1), 231-238.

Vonk, J., & MacDonald, S. E. (2004). Levels of abstraction in orangutan (Pongo abelii) categorization. *Journal of Comparative Psychology, 118*(1), 3.

Washburn, D. A., & Rumbaugh, D. M. (1992). Testing primates with joystick-based automated apparatus: Lessons from the Language Research Center’s Computerized Test System. *Behavior Research Methods, Instruments, & Computers, 24*(2), 157-164.

Wasserman, E. A., Wasserman, E. A., & Zentall, T. R. (2006). *Comparative cognition: Experimental explorations of animal intelligence*: Oxford University Press, USA.

Webb, B. (2012). Cognition in insects. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2715-2722.

Webb, S. J. N., Hau, J., & Schapiro, S. J. (2019). Relationships between captive chimpanzee (Pan troglodytes) welfare and voluntary participation in behavioural studies. *Applied animal behaviour science, 214*, 102-109.

Wood-Gush, D., & Vestergaard, K. (1991). The seeking of novelty and its relation to play. *Animal behaviour, 42*(4), 599-606.

Zajonc, R. B. (1965). Social Facilitation: A solution is suggested for an old unresolved social psychological problem. *Science, 149*(3681), 269-274.

Title Chapter 2:

Lab cognition going wild: Implementing a new portable touchscreen system in vervet monkeys

Rachel A. Harrison[a, b*†], Tecla Mohr[a, b, c, †], & Erica van de Waal[a, b, c]

[a] Department of Ecology & Evolution, University of Lausanne, Lausanne, Switzerland

[b] The Sense Innovation and Research Center, Lausanne and Sion, Switzerland

[c] Inkawu Vervet Project, Mawana Game Reserve, South Africa

[†] These authors contributed equally to this paper

* Corresponding author: rachelh363@gmail.com / rachel.harrison@unil.ch (R.A.H.)

Abstract

1. Touchscreen technology has provided researchers with opportunities to conduct well-controlled cognitive tests with captive animals, allowing researchers to isolate individuals, select participants based on specific traits, and control aspects of the environment.

2. In this study, we aimed to investigate the potential utility of touchscreen technology for the study of cognition in wild vervet monkeys. We assessed the viability of touchscreen testing by comparing rates of participation between wild and sanctuary-housed vervets. Additionally, we compared performance on a simple associative learning task in order to verify that wild participants are able to engage meaningfully with a touchscreen task presented in their natural environment.

3. We presented eight groups of vervet monkeys (four wild and four sanctuary groups, totalling 240 individuals) with a portable touchscreen device. The touchscreen displayed tasks in which food rewards could be gained by touching a stimulus displayed on the screen. We assessed individuals' likelihood of interacting with the touchscreen, their frequency of participation, and their performance on a simple associative learning task.

4. We found that sanctuary-housed monkeys were more likely to interact with the touchscreen. Participation in wild vervet monkeys was influenced by sex and age. However, monkeys in the two contexts (sanctuary vs. wild) did not differ in their performance on a simple associative learning task.

5. This study demonstrates that touchscreen technology can be successfully deployed in a population of wild primates. This gives us a starting point to test animal cognition under natural conditions that include varying group composition, environmental challenges, and ongoing activities such as foraging, which are challenging to recreate in captivity. While rates of participation were lower than those found in captivity, reasonable sample sizes can be achieved, and wild primates can successfully learn touchscreen tasks in a manner comparable to their captive counterparts.

Keywords:

Touchscreen field experiment - Captivity effect - Free time hypothesis - Participation Cognitive task - Vervet monkey

1. Introduction

In recent years, while many experiments have been done to quantify both within and between-species differences in cognition, most have been conducted in captive environments such as zoos (see Hopper, 2017, for review) or laboratories, with relatively few conducted in the wild (Martin et al., 2022; Pritchard et al., 2016). In captivity, researchers can control environmental factors, animals can be isolated from the rest of the group and can be sampled based on individual characteristics. Research conducted in captivity raises two key questions; how representative is the cognition of captive animals in comparison to their wild counterparts, and if there are differences, from where do they stem? Identifying the ways in which captive animals' cognitive abilities may differ from those of wild animals could provide an insight into the extrinsic and intrinsic factors influencing performance on cognitive tests. To answer these questions, it is necessary to find ways to study animal cognition in the wild in a manner that is comparable to captive tests of cognition.

1.1 Studying cognition in the wild

There has been an increase in cognitive experiments conducted in the wild since Matsuzawa's pioneering 'outdoor laboratory' at the chimpanzee field site Bossou (Matsuzawa, 1994), along with improvements in the methods and technology used (Szabo et al., 2022). Cognitive experiments have been conducted with wild subjects across a wide range of taxa, from spatial cognition in wild rufus hummingbirds (Selasphorus rufus, Healy & Hurly, 2013), innovative problem solving in wild meerkats (*Suricata suricatta*: Thornton & Samson, 2012), to reversal learning in wild vervet monkeys (*Chlorocebus pygerythrus*: Kumpan et al., 2020). These studies have the benefit not only of complementing existing research into cognition in captive animals, but additionally testing animals within their natural context, with the ecological pressures that it entails (Harrison & van de Waal, 2022). A challenge of conducting cognitive research in wild populations is finding methods which can be deployed in the field and produce comparable data to captive studies. One possibility, explored in the current study, is the use of touchscreen technology.

1.2 Touchscreens in cognitive testing

Touchscreens have been used in captivity to examine cognitive processes including memory, decision making, associative and reversal learning, and collaboration (Egelkamp & Ross, 2019). There are already many examples of cognitive testing using touchscreens in captive primates (Martin et al., 2022). For example, touchscreens have been used to test working memory in captive chimpanzees (Inoue & Matsuzawa, 2007; Kawai & Matsuzawa, 2000), risk-taking in chimpanzees, gorillas (*Gorilla gorilla gorilla*) and Japanese macaques (*Macaca fuscata*, Leinwand et al., 2020) and in-group recognition in capuchin monkeys (*Sapajus apella* ,Pokorny & de Waal, 2009). While touchscreens could be an innovative device to test wild animals, they bring technical challenges, namely the potential lack of electricity and Wi-Fi connection outside of captive environments (Schmitt, 2019). On the other hand, studying animals under unnatural conditions, such as small group sizes, isolation, and close contact with humans, affects their behaviour (Forss et al., 2022; Seferta et al., 2001; Woolverton et al., 1989), suggesting that researchers should explore the potential of using innovative testing methodologies to compare wild and captive performance in cognitive tasks. In order to validate new methods for testing cognition comparatively in the wild and captivity, it is important to understand likely participation levels as well as comparing cognitive performance, as cognitive performance can only be assessed in individuals which participate in testing (van Horik et al., 2017).

1.3 Participation in experiments: the 'free time' and necessity hypotheses

There are alternative hypotheses to explain different rates of participation in experimental tasks between individuals. The 'free time' or 'excess energy' hypothesis suggests that individuals will engage in exploration when they are under less pressure to find key resources or evade predators (Kummer & Goodall, 1985). The 'necessity hypothesis' in contrast, predicts that animals will become more motivated to explore and innovate when resources are lacking, forcing them to find alternative solutions to access food sources (Grund et al., 2019). The day-to-day behaviour of wild animals is strongly influenced by needs introduced by their social and physical environment which vary seasonally and may not be present to the same extent in captive animals (Cauchoix et al., 2017). These needs may restrict the 'free time' individuals have to participate in cognitive testing. Furthermore, in many primate species, individuals need to travel to find daily resources, giving researchers less time in a fixed location to present an experimental apparatus. In captivity, animals often have free access to food and water, reducing the need for foraging time, which may give them more opportunity to interact with the experimental paradigm.

Some studies have indeed shown higher rates of exploration of novel objects and higher persistence in captive animals in comparison to wild ones (Benson Amram et al., 2013; Forss et al., 2015), suggesting that captive individuals should interact with and explore experimental paradigms more than wild individuals. Rates of participation in wild populations may also be low, with Morand-Ferron et al. (2015) finding that in a population of wild great tits (*Parus major*) only 8% visited and interacted with an artificial feeder. Alongside differences between wild and captive populations, experiments have also shown high inter-individual variability in interaction with experimental tasks, with factors such as age and level of distraction influencing an individual's likelihood of interacting with a task (Martina et al., 2021).

1.4 Individual differences in participation: Age and sex

Research across multiple species has shown that juveniles are more likely to explore novel objects than adults (Biondi et al., 2010; Morand-Ferron et al., 2015) and are more persistent when solving novel problems (Benson Amram et al., 2013), spending more time in proximity to novel tasks (Kendal et al., 2005). Results such as these suggest that juveniles may be less neophobic and more motivated to explore and discover their environments than adults, and therefore show higher levels of participation in novel cognitive tasks.

Other studies have focused on differences in exploration and innovation between the sexes. Many species are sexually dimorphic in body mass, with males being larger and stronger than females, which results in task monopolization by males (Bean, 1999; van Horik et al., 2017). In a scrounging test in vervet monkeys, males, who are larger and stronger than females, obtained more food by participating more and displacing others from artificial food patches (Li et al., 2021). In group-testing paradigms, in which individuals must compete to access a task rather than being offered it individually, the larger sex may therefore be more likely to participate.

Understanding and quantifying differences in levels of participation in novel tasks is critical for two reasons: firstly, this can aid in study design, allowing researchers to predict which age classes are more likely to participate in a task, and potentially design paradigms to encourage participation in less well-represented groups. Secondly, this gives an insight into intra-species differences in factors such as neophobia, risk-taking, and motivation.

1.5 The captivity effect and performance in cognitive tests

Beyond participation in cognitive tests, some studies have found differences in performance between captive and wild subjects (see McCune et al., 2019, for review). Whilst these studies are limited in number, the majority have found enhanced performance in captive subjects in comparison with wild subjects (e.g. Benson Amram et al., 2013), and within primates, it has been suggested that increased exposure to humans enhances problem-solving capacities (Damerius et al., 2017; Forss et al., 2020).

However, some studies have found the opposite, with wild subjects performing equally well as (Cauchoix et al., 2017) or outperforming (McCune et al., 2019) wild-caught subjects temporarily held in captivity, though it is unclear how the stress of time spent in captivity might influence the performance of wild-caught subjects.

The tests deployed in comparisons of wild and captive cognition have so far been varied. Associative learning appears to be a good target for those interested in the evolution of cognition, as it is highly conserved but also demonstrates large inter-specific and intra-specific differences in performance, and is likely to have fitness consequences (Morand-Ferron, 2017; Morand-Ferron et al., 2016; Raine & Chittka, 2008). Currently, there is little evidence regarding the causal links between cognitive ability and fitness in wild populations; measuring performance in associative learning tasks and then relating this to functional mechanisms would be one route to elucidating these causal relationships (Cole et al., 2012; Morand-Ferron et al., 2015). Equally, examination of whether the associative learning abilities of wild animals are similar to those of animals tested in captivity may give some insight into the developmental processes and evolutionary pressures that influence this ability, including the role of social context and sociality. Testing both captive populations and wild populations with varying group sizes may provide some insight into the impact of social context upon problem solving. If links can also be made between cognition and fitness in wild populations, this could provide support for the social intelligence hypothesis that posits large group sizes drive cognitive evolution (Dunbar, 1998), as demonstrated in a study of the effect of group size on cognition in wild pinyon jays by Ashton et al. (2018).

1.6 Aims and hypotheses

The current study had two major aims; firstly, to disentangle the effects of environmental factors and individual traits on participation rates of wild and sanctuary vervet monkeys in cognitive testing, and secondly, to provide the first results of a simple associative learning task comparing the performance of sanctuary and wild vervet monkeys. To do this, we adopted a multi-step training procedure using portable touchscreen technology (Schmitt, 2018). We conducted an experiment with the aim of training both wild and sanctuary vervet monkeys living in social groups in South Africa (wild: four groups at the Inkawu Vervet Project (IVP); sanctuary: four groups at the Wild Animals Trauma Centre & Haven (W. A. T. C. H.)) to interact with the screen (using a visual stimulus, a blue square, that had to be touched to gain a food reward). In this paper, we analyse rates of participation across multiple tasks presented on the touchscreen and present the first results stemming from one of these tasks; a simple associative learning task. Our hypotheses are outlined below and summarised in Table. 1.

First, we investigated the likelihood of participation in two environmental contexts (wild and captivity). Our hypothesis was in line with the ‘free time’ hypothesis (Kummer & Goodall, 1985). The lack of danger and the free time available in captivity should provide sanctuary vervet monkeys with more opportunities to interact with the touchscreen compared to wild vervet monkeys. The sanctuary groups tested also had in general smaller group sizes than the wild groups, and so reduced competition for the task is also likely to result in increased likelihood of participation.

Secondly, we investigated the impact of two individual traits: age and sex, on the likelihood of wild monkeys participating in the experiment. In vervet monkeys, juveniles are more explorative and less neophobic than adults (Forss et al., 2021). In line with this evidence, we expected higher curiosity and greater participation from juvenile vervet monkeys compared to adults. Following findings in previous studies described above (Bean, 2001; Li et al., 2021; van Horik et al., 2017), adult male vervet monkeys, being larger than adult females, could be expected to have higher rates of participation. However, co-dominance was found in the same study groups at IVP (Hemelrijk et al., 2020), and adult females as core group members have been trained as models in multiple field experiments (Borgeaud & Bshary, 2015; Botting et al., 2018; Gareta García et al., 2021; van de Waal et al., 2015). Thus, we also have evidence leading us to expect a high monopolization of the apparatus by adult females and for this reason we do not have a clear hypothesis concerning higher likelihood of participation in one sex or the other. We also explored the effect of previous rewards on individuals’ likelihood of participation. We expected individuals to be more likely to participate if they had previously been rewarded for interactions with the touchscreen.

In the wild population, we also explored the effect of age and sex upon the *rate* of participation. Age was expected to influence the number of attempts made at the task; we expected juveniles to make more attempts than adults. However, an individual’s ability to monopolise the task is also expected to influence the number of attempts made in a session, and adults may be better able to outcompete others for access than juveniles.

Finally, we tested the cognitive abilities of both wild and sanctuary monkeys on a simple associative test (the speed of learning to touch a blue square presented on the screen to attain a reward). Following evidence of a captivity effect in problem solving in primates (Forss et al., 2020), we expected that sanctuary monkeys would require fewer trials to reach criterion on the associative task.

Table. 1. Summary of comparisons and predictions

Outcome	**Comparison**	**Prediction**	**Sample size**
Likelihood of participation	Wild vs. sanctuary	Higher in sanctuary	$N_{\text{Wild}} = 178$ $N_{\text{Captive}} = 62$
	Sex and age classes within wild population	Higher in juveniles	N = 178 (wild only): $N_{\text{AdultFemale}} = 53$* $N_{\text{AdultMale}} = 40$* $N_{\text{JuvenileFemale}} = 43$* $N_{\text{JuvenileMale}} = 55$*
Rate of participation	Sex and age classes within wild population	Higher in juveniles	N = 86 (wild only): $N_{\text{AdultFemale}} = 23^{\dagger}$ $N_{\text{AdultMale}} = 19^{\dagger}$ $N_{\text{JuvenileFemale}} = 20^{\dagger}$ $N_{\text{JuvenileMale}} = 26^{\dagger}$
Task performance – simple association learning	Wild vs. sanctuary	Faster in sanctuary	$N_{\text{Wild}} = 15$ $N_{\text{Captive}} = 8$

* Note: Thirteen individuals were tested as both juveniles and adults over the course of the study.

† Note: Three individuals participated as both juveniles and adults over the course of the study.

2. Material and methods

2.1 Study site and species

Data were collected from May 2019 to January 2022 on four groups of wild vervet monkeys (Ankhase, Baie Dankie, Kubu, and Noha) at the Inkawu Vervet Project (IVP) in Mawana Game reserve, South Africa, and from August 2018 to January 2022 on four groups of sanctuary vervet monkeys (Boeta, Cowen, Liffie, and Poena) at the Wild Animals Trauma Centre & Haven (W. A. T. C. H.), South Africa. Group size varied from three to 65 individuals (for detailed group composition see Table. S1). Females were defined as adults when they reached five years old or when they first gave birth (whichever occurred first); we defined males as adults when they reached five years old or upon dispersal from their natal group (whichever occurred first). Individuals were defined as juveniles from the age of four months until they reached adulthood. Babies (individuals aged less than four months during testing) were excluded from the dataset as they were not independent from their mothers. For total sample composition, see Table. S2.

2.2 Ethical statement

Our study adhered to the ASAB/ABS Guidelines for the use of animals in research (ASAB/ABS, 2020) and was approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa.

2.3 Subjects

Since 2010, six neighbouring groups of wild vervet monkeys have been habituated to humans and their artefacts at the IVP. Researchers individually identify individuals by face and body characteristics. The size of the four studied wild groups at the IVP during the study period varied between 15 and 65 individuals (see Table. S3). Vervet monkeys are semi-terrestrial, which, coupled with their opportunistic nature, allows researchers to observe them easily and to test them with field experiments (Mertz et al., 2019). Monkeys in the four groups which participated in the current study have previously participated in behavioural experiments involving artificial foraging tasks (e.g. Bono et al., 2018; Canteloup et al., 2020; van de Waal et al., 2015).

At the sanctuary, groups are composed of individuals with different backgrounds (including orphans, monkeys rescued from roadsides or street-markets, or injured individuals) and live in four large outdoor enclosures in social groups of 3- 21 individuals (see Table. S3). The majority of individuals arrived at the sanctuary as infants and were initially cared for by humans before being integrated into mixed-age social groups at three months old. Water and food are continuously available during the day. One group (Liffie) was released after the first year of experiments (November 2019), while the other three groups (Boeta, Cowen, Poena) were studied until February 2022. The last three groups participated in novel object experiments (Forss et al., 2021). While other behavioural research has previously been conducted at the sanctuary (van de Waal et al., 2013; van de Waal & Whiten, 2012) none of the groups included in the current study had participated in other studies beyond that of Forss et al. (2021).

2.4 Material and Procedure

We used a portable touchscreen (**Z**oo based-**A**nimal-**C**omputer-**I**nteraction System, ZACI; Figure. 1S) that has been built to conduct research on apes in zoos (Schmitt, 2018). Whilst originally intended for studying animals in captivity, we adapted this portable touchscreen for field usage. To allow distance between the researcher and the animals, a convertible laptop was connected by a hotspot to an operating tablet from which we could control the program. The experiment was written in Matlab using Psychophysics Toolbox extensions (Brainard, 1997). The code records the identity of the individual participating (manual input), the type of stimuli used in the task (manual input), the number of trials attempted, the area in which each stimuli was presented on the screen, and whether the response was correct or not (coded as 1, 0). To reward participants for each correct touch, the code sends an input to an electronic control unit (ECU) composed of a rechargeable battery and attached to a food dispenser (Model ENV-203-190IR, by Med Associates Inc St. Albans) ejecting soaked corn kernels. Researchers carried the touchscreen into the field for the experiment, attached it to a tree, and removed it immediately following each day of testing (Figure. 1). The experimenter(s) maintained a distance of at least five metres from the task. At the sanctuary, we attached the portable touchscreen to the enclosure using hooks. The experiment started immediately after attaching the device. We recorded each experiment using one camera (JVC EverioR Quad Proof GZ-R415BE) fixed on a tripod. All sanctuary data was collected by TM, with wild data collected by TM and six field assistants who followed the same protocol as TM. TM and all field assistants involved in data collection were required to pass an identification test prior to the start of the study in which they had to repeatedly and accurately identify every monkey in the group they were working with.

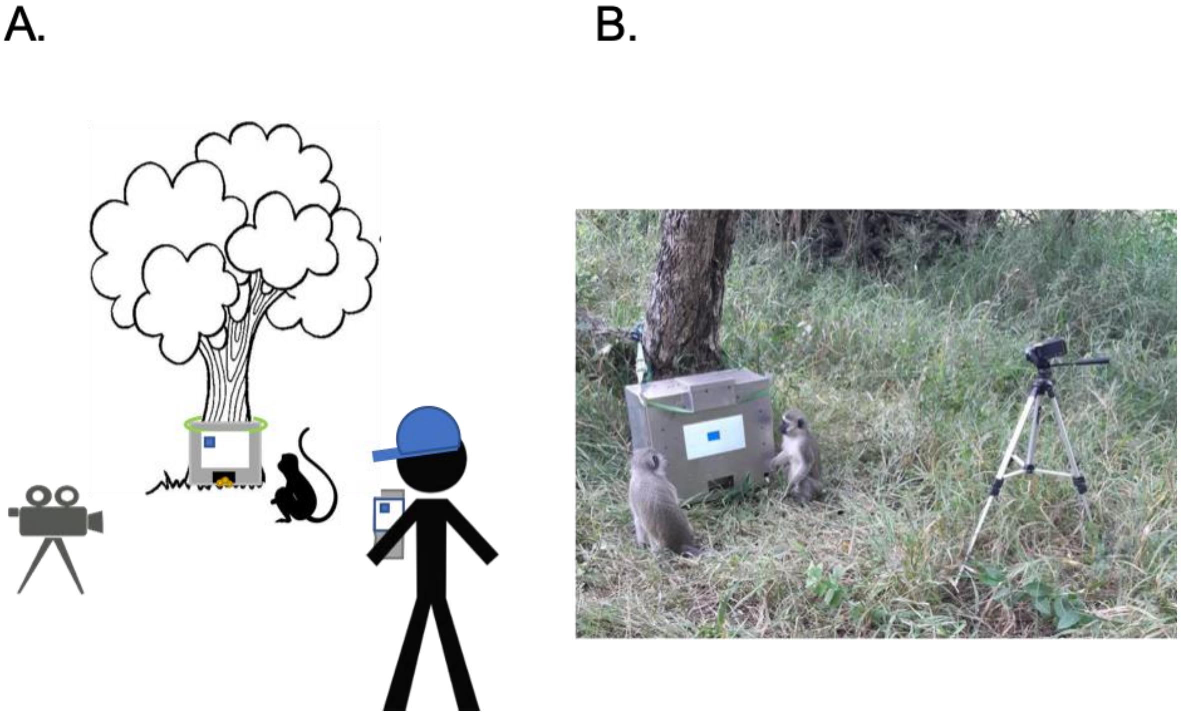


Figure. 1: A) A schematic representation of an experimental setup in the field (Mawana). B) Monkeys interacting with the touchscreen at their sleeping site.

We trained monkeys using three training tasks based upon the presentation of a blue square on a white background (Figure. 2). In Task 1 (Habituation phase) we presented a blue square in the centre of a screen, with a white background. Monkeys received a reward if they touched either the blue square or the white background. We considered this first habituation phase completed when subjects sat in front of the screen and interacted with the touchscreen. Once the monkeys completed Task 1, we used the same image (central blue square on a white background) to test Task 2. In Task 2, monkeys were rewarded only when they touched the blue square. In Task 3, the blue square changed position in each trial, and again monkeys were only rewarded for touching the blue square. From Task 2 onwards, monkeys had to reach the learning criterion of seven correct touches out of 10 touches in three consecutive sets, eight correct touches out of 10 touches in two consecutive sets, or nine correct touches out of 10 touches in one set (learning criterion from Paula et al., 2019; Salwiczek et al., 2012). When individuals made incorrect touches in Tasks 2 and 3 the blue square remained in the same location on the screen. The training was followed by two classical associative learning tasks (classical associative learning, CAL; reversal classical associative learning, RCAL) based upon the presentation of two stimuli of different shape, colour, and patterns on the screen (see Supplement for further information – CAL and RCAL testing made up 16% of recorded attempts at the task in the current dataset; 424 / 2547 attempts). These tests were included when measuring participation, but more detailed analyses of performance are not within the scope of this paper. For each correct touch, subjects received three to four corn kernels as a reward. Individuals were allowed to participate with up to 30 touches divided into three sets of 10 touches in the first three tasks, while they were allowed to participate only up to ten touches in the CAL and RCAL tasks, after which a black screen was displayed to prevent further interaction. All trials (correct and incorrect) were automatically recorded. There was an inter-trial interval of two seconds regardless of whether the previous choice was correct (there was no punishment in the form of increased inter-trial interval for an incorrect choice).

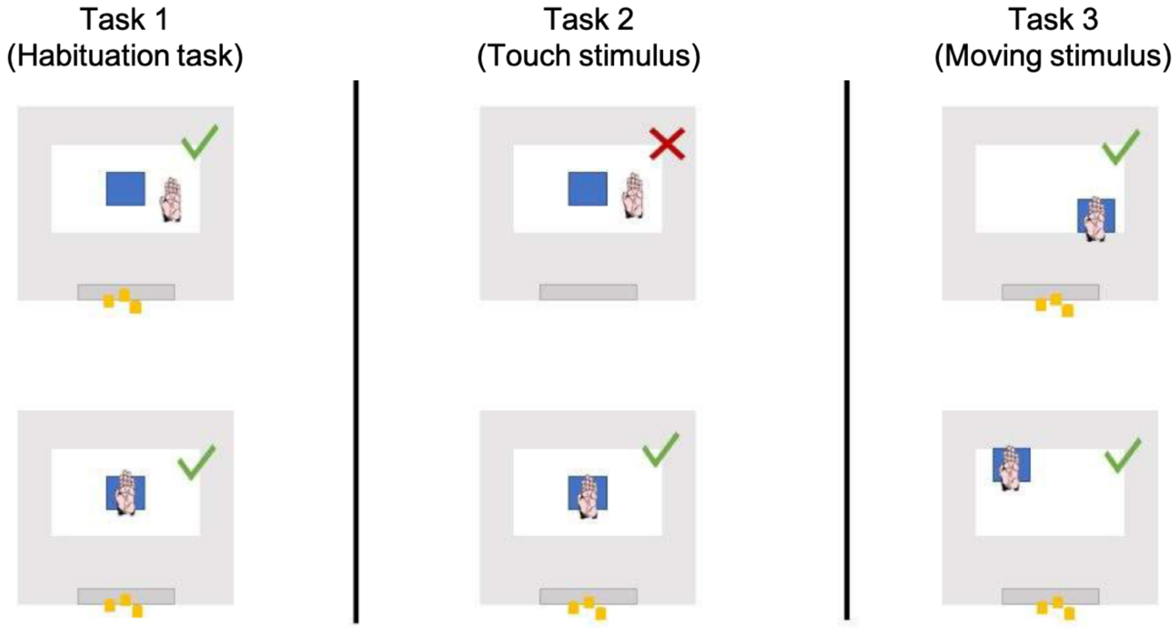


Figure. 2. Three training tasks from left to right in Task 1 (habituation task) monkeys had to touch anywhere on the screen (white background and blue square); in Task 2 (touch stimulus), monkeys had to touch the blue square in the middle of the screen. In Task 3 (moving stimulus), monkeys had to touch the blue square as in Task 2, but for each correct touch the square changed position on the screen. The hand shown in the pictures represents the monkeys' touches (potentially correct or incorrect, as shown by ticks and crosses) and the yellow dots represent the corn reward. Figure: Lucas Zermatten.

We presented the touchscreen approximately twice a week both at the sanctuary and in the wild. For wild groups, the experiment was stopped when all members of the group moved away or stopped interacting. Experimental sessions were occasionally stopped due to technological problems, interruptions by sanctuary staff, storms, or other possible factors that could distract the monkeys' attention. Excluding these sessions, the wild monkeys were exposed to the device for a minimum session duration of 6.82 minutes, and a maximum duration of 187.43 minutes (mean session duration = 61.67 minutes). At the sanctuary the monkeys were exposed to the device for a minimum test session duration of 5.9 minutes and a maximum duration of 193.43 minutes (mean session duration = 31.95 minutes). See Supplemental Table S4 for a summary of the total number of test sessions conducted per group, and Supplemental Table S5 for the total presentation time per group. Due to the COVID-19 pandemic, there were occasionally longer breaks in testing, meaning that the interval between test sessions ranged from zero to 310 days in the wild and one to 426 days in the sanctuary (the length of time between test sessions did not significantly impact individuals' likelihood of participation, see Supplemental Information: Additional analyses: Effect of breaks in testing for details).

2.5 Pilot testing in the sanctuary groups

Three of the four sanctuary-housed groups (Liffie, Poena, and Boeta) participated in pilot testing from August 2018 – November 2018. During these pilot sessions (N = 155 test sessions), monkeys were exposed primarily to Task 2, with three individuals participating in Task 3. Following this pilot, changes were made to the size of the touchscreen and to the positioning of the infrared device to achieve greater accuracy in recording correct and incorrect touches. Data from this pilot testing are included in the current dataset when comparing participation rates between wild and sanctuary groups in which participation is a binary measure, thus allowing us to compare likelihood of participation from individuals' first exposure to the task onwards. For this comparison, accurate counts of correct and incorrect touches are not required, and so the data collected in the pilot sessions is comparable with data collected during the main test period. Individuals which received Task 3 during these pilot sessions were excluded from our analysis of performance on this task, due to potential differences in their training experience in comparison with individuals who received this task for the first time during the main test period.

2.6 Statistical analyses

All analyses were performed using R (R Core Team, 2020) and RStudio (RStudio Team, 2020). Generalised linear mixed models (GLMMs) were used to analyse individuals' likelihood of participation in the task, the effect of previous success on the likelihood of an individual participating, and the number of trials individuals required to reach criterion in Task 3. Binary participation in the touchscreen task was assessed using binomial GLMMs with logit link function (function 'glmer' in the R package lme4; Bates et al., 2014) and the optimizer "bobyqa". The number of attempts individuals made per session was analysed using a Cox proportional hazards model (function "coxme" in the R package coxme; Therneau, 2015), to account for right-censored data. The number of attempts each individual made before reaching criterion in Task 3 was assessed using a negative binomial GLMM with a log link (function 'glmmTMB' in the R package glmmTMB; (Magnusson et al., 2017). A negative binomial distribution was used to account for significant overdispersion in the data.

In two analyses (likelihood of participation and trials required to pass Task 3), comparison was made between wild and sanctuary populations. The wild and sanctuary populations were not comparable in terms of age and sex classes, and so further analyses exploring the impact of these factors upon task participation were limited to the wild population only.

A binomial GLMM (Analysis 1) was used to compare the likelihood of sanctuary and wild individuals participating in the tasks (with participation in each session coded as 1 or 0) with Context (wild vs. sanctuary), and Session Duration (z-transformed) as predictor variables. This analysis included all touchscreen tasks (Tasks 1 – 3, CAL and RCAL) and included all individuals present in the groups at the time of testing (total: N = 240; wild: N = 178; sanctuary: N = 62) with random effects for both Individual and Group (unnested, as some individuals moved between groups over the course of the experiment). Sessions which were terminated early due to external factors were not included in this analysis, as individuals were potentially prevented from participating during these sessions and so they may not reflect how many individuals would have participated had the session continued uninterrupted. Eighty-seven sessions were excluded for this reason, leaving 675 experimental sessions in the analysis. See Table. S4 for a breakdown by group of the number of uninterrupted test sessions included in this analysis.

A binomial GLMM (Analysis 2) was used to investigate the impact of individual factors such as age and sex upon participation in the task in the wild population only. Participation in each session was coded as 1 or 0, with Age Class (juvenile vs. adult), Sex (female vs. male), Group (N = 4), and Session Duration (z-transformed) as predictor variables, with an interaction between Age Class and Sex. Individual identity was included as a random effect. This analysis included all touchscreen tasks (Tasks 1 – 3, CAL and RCAL) and included all individuals present in the groups at the time of testing (N = 178). As in GLMM 1, sessions which were terminated early due to external factors were not included.

A mixed-effects survival model (Analysis 3) was used to investigate the impact of individual factors upon the number of attempts made by individuals per session within wild groups, with Sex, Age Class, and Group as predictor variables, and a random effect of Individual. This analysis included data from Tasks 2 and 3 only, as the experimental procedure of allowing only 30 attempts per session was applied most consistently for these tasks. Only individuals that participated in Tasks 2 and 3 were included in this analysis (N = 86). Prior to running the analysis, any individuals who had participated beyond 30 attempts had their number of attempts truncated at 30. We fitted a Cox proportional hazards model as these models are appropriate for right-censored data, in which an experimental cut-off point prevents further data collection. In our case, as many individuals were prevented from making more than 30 attempts per session, we do not have data showing the upper limit of how many attempts an individual would have made without this limit. This model therefore analysed the likelihood of an individual ceasing to participate prior to making 30 attempts. The Cox model produces hazard ratios (HR), in which an HR > 1 indicates a positive relationship between a variable and event probability, and an HR < 1 indicates a negative relationship between a variable and event probability. In our case, an HR above one indicates that an individual was more likely to stop participating sooner (i.e. to make fewer attempts), while an HR below one indicates an individual was more likely to approach 30 attempts without ceasing to participate.

The effect of previous success on wild individuals' likelihood of participation in the next test session was analysed using a binomial GLMM (Analysis 4). Age Class, Sex, Group and Session Duration (z-transformed) were included as predictors, with an interaction between Age Class and Sex, and a random effect of Individual. The effect of previous success was analysed by including as a predictor variable the number of rewards an individual had received the previous time they participated, with this value resetting to NA if more than 30 days had passed since the group had received the touchscreen. As only individuals who had interacted with the touchscreen at least once had a previous reward value, the sample size for this analysis was limited to 94 individuals.

A negative binomial GLMM (Analysis 5) was used to analyse the number of trials taken to pass Task 3 in the 23 individuals (wild: N = 15, sanctuary: N = 8) who achieved this, with Context as a predictor variable, and a random effect of Group. Some individuals in the Sanctuary (N = 3) had been trained with Task 3 during an initial pilot testing period (2018), during which the size of the blue square presented on the screen was larger and the infrared technology used to count the number of correct and incorrect touches was still being calibrated. These individuals were excluded from the analysis due to the difference in their training experience and concerns regarding the accuracy of measurement of the number of trials they had completed.

For full details of all diagnostic checks performed on the above models, see Supplemental Information “Model Assessment”.

3.Results

3.1 Analysis 1: Likelihood of participating in the task, sanctuary vs. wild

The full model (Analysis 1) was a significantly better fit to the data than a null model containing only the random effects structure (χ^2 =187.54, p < 0.0001). Context had a significant effect upon individuals’ likelihood of participating in the touchscreen task (Figure. 3, Table. 2). A main effect of Context indicates that Sanctuary individuals were significantly more likely to participate than wild individuals (β = 1.96, p = 0.002). Furthermore, the analysis indicates that the duration of the session has an impact on the likelihood of participation. Specifically, a longer session is associated with a higher probability of participation (β = 0.48, p < 0.0001).

Table. 2. Results of a GLMM predicting individual participation in the task in wild and sanctuary groups.

Effect	**Estimate**	**Wald 95% confidence interval**	***p*-value**
Intercept	-4.05	-4.82; -3.28	
Context (Sanctuary)	1.96	0.74; 3.18	0.002
Session Duration (z-transformed)	0.48	0.41; 0.55	< 0.0001

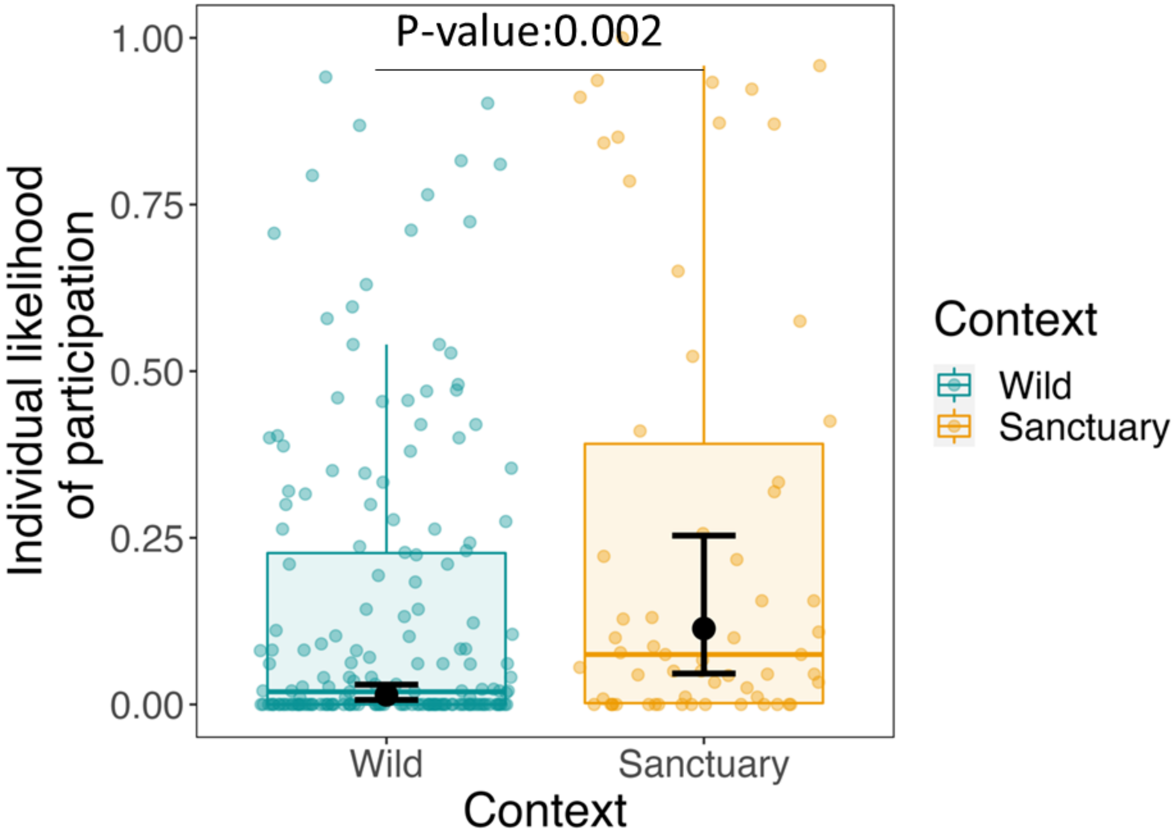


Figure. 3. Model predictions (estimated marginal means) of the effect of Context on likelihood of participation in the task. The solid black point shows the prediction for each Context, with black error bars showing the 95% confidence interval. The prediction is at the mean session duration. Boxplots show the distribution of the observed likelihood of participation. The solid horizontal line, coloured by Context, shows the median proportion of sessions in which individuals participated. Upper and lower limits of the box show the first and third quartiles, and whiskers extend to the highest and lowest values at 1.5 times the interquartile range. Coloured points show the observed proportion of sessions in which each individual participated, with each point representing one individual.

3.2 Analysis 2: Likelihood of participation in the task, individual factors in the wild population

The full model was a significantly better fit to the data than a null model containing only the random effect structure ($\chi^2 = 229.1$, $p < 0.0001$). The likelihood of participation varied by both age and sex (see Table. 3, Figure. 4). Adult females were more likely to participate than juvenile females ($\beta = 0.77$, $p = 0.014$), while the contrary effect was seen in males, who were less likely to participate as adults than as juveniles (Age Class * Sex interaction: $\beta = -3.42$, $p < 0.0001$). Juvenile males were more likely to participate than juvenile females ($\beta = 1.58$, $p = 0.016$).

Table. 3. Results of a GLMM predicting the likelihood of participation by individuals per session in the task in the wild population.

Effect	**Estimate**	**Wald 95% confidence interval**	***p*-value**
Intercept	-3.31	-4.68; -1.95	
Age Class (Adult)	0.77	0.16; 1.38	0.014
Sex (Male)	1.58	0.29; 2.86	0.016
Group (Baie Dankie)	-2.37	-3.84; -0.90	0.002
Group (Kubu)	-2.27	-3.78; -0.76	0.003
Group (Noha)	-1.14	-2.42; 0.14	0.080
Session duration (z-transformed)	0.4	0.40; 0.55	< 0.0001
Age Class * Sex	-3.42	-4.62; -2.21	< 0.0001

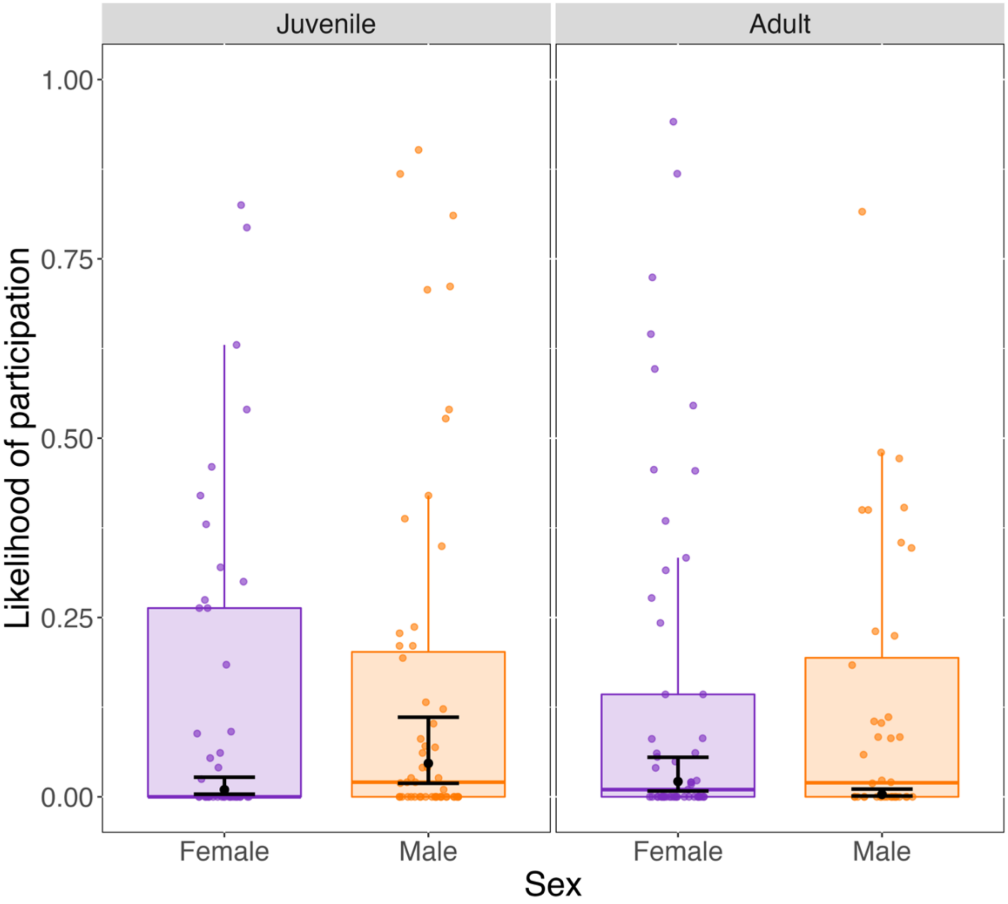


Figure. 4. Model predictions (estimated marginal means) of the effect of Age Class and Sex on likelihood of participation in the task in the wild population, shown by age sex class. The predicted value for each Sex and Age Class category is shown by the solid black point, with error bars showing the 95% confidence interval around this prediction. The prediction is at the mean Session Duration. Boxplots show the distribution of the proportion of sessions participated in by each age-sex class, with solid horizontal lines showing the median proportion, upper and lower limits of the box showing the first and third quartiles, and whiskers extending to the highest and lowest values at 1.5 times the interquartile range. Points show the proportion of sessions participated in by each individual, coloured by Sex.

Group also impacted individuals' likelihood of participation (overall significance calculated using the 'Anova' function in the package 'car': $\chi^2 = 14.23$, p = 0.003). A post-hoc Tukey test revealed that individuals in Baie Dankie (β = -2.37, $\underline{p}$ = 0.008) and Kubu (β = -2.27, p = 0.016) were significantly less likely to participate than those in Ankhase. No other significant between-group differences were found.

3.3 Analysis 3: Number of attempts made in the task, individual factors in the wild population

The full model was a significantly better fit to the data than a null model containing only the random effect of individual ($\chi^2 = 14.83$, p = 0.02). No effect of Sex or Age Class was found, but there was a main effect of Group ($\chi^2 = 8.73$, p = 0.033). A post-hoc Tukey test, however, indicated that there was only a marginal, non-significant, difference between Noha and Baie Dankie (HR = 0.53, p = 0.060), indicating that individuals in Noha tended to make more attempts at the task than individuals in Baie Dankie.

While not significant, both Sex and Age Class influenced the number of attempts made per session by individuals. Male juveniles were more likely to reach 30 attempts in a session than female juveniles (HR = 0.59, p = 0.061, see Figure. 5). There was also a non-significant interaction between Age and Sex, such that male adults were more likely to stop participating before reaching 30 attempts than were male juveniles (HR = 2.00, p = 0.086). Caution should be taken in interpreting these non-significant effects, but it is possible that with a larger sample size significant sex and age differences in individuals' rate of participation would be found.

Table. 4. Results of a Cox mixed effects model predicting the number of attempts made by individuals per session in the task in the wild population.

Effect	**Hazard Ratio**	**Standard error**	**p-value**
Sex (Male)	0.59	0.28	0.061
Age Class (Adult)	0.80	0.28	0.430
Group (Baie Dankie)	1.89	0.29	0.029
Group (Kubu)	1.72	0.37	0.140
Group (Noha)	1.00	0.29	0.990
Interaction: Age Class x Sex	2.00	0.41	0.086

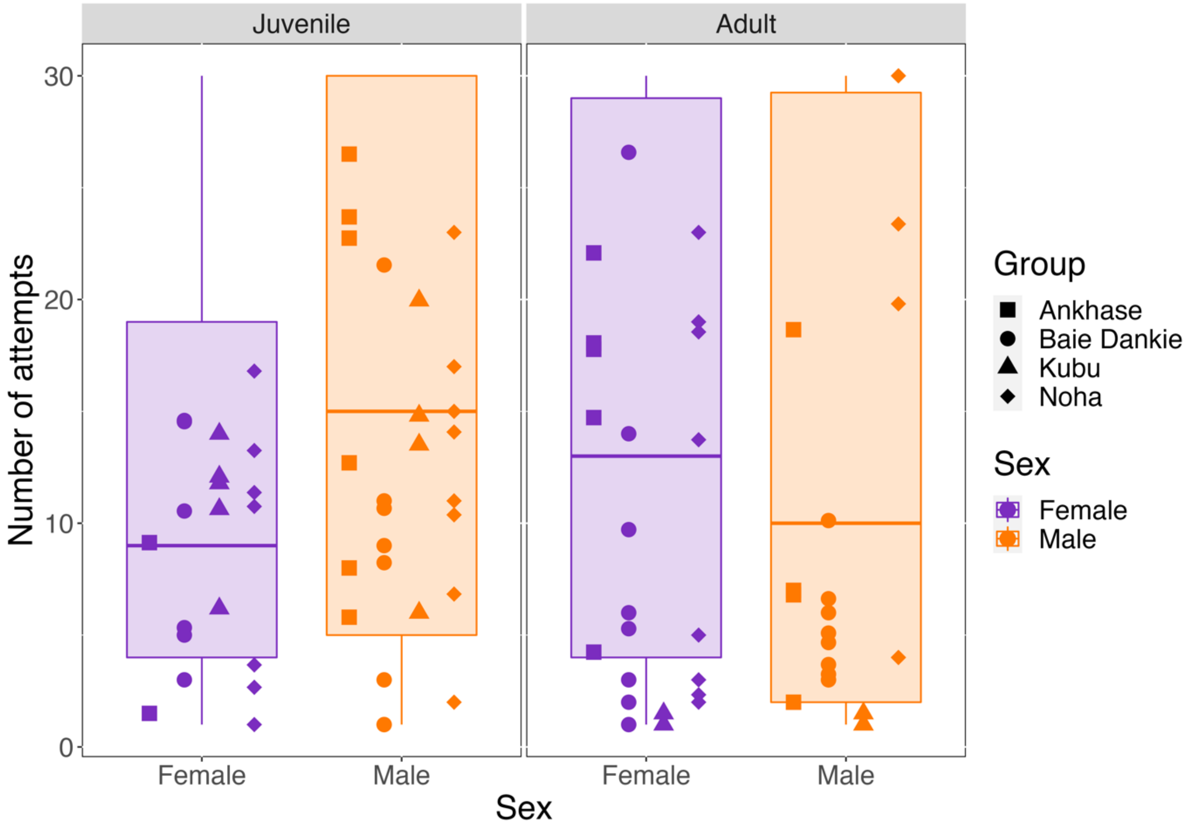


Figure. 5. The number of attempts made by individuals in the wild population. Boxplots, colored by sex, show the distribution of the number of attempts made by each age-sex class, with solid lines showing the median number, upper and lower limits of the box showing the first and third quartiles, and whiskers extending to the highest and lowest values at 1.5 times the interquartile range. Solid points show the mean number of attempts made per session by each individual, coloured by Sex with shape indicating Group membership.

3.4 Analysis 4: Effect of previous success in the wild population

The full model (Analysis 4) was a significantly better fit to the data than a null model containing only the random effects structure (χ^2 = 205.35, p < 0.0001). As in the previous analysis of likelihood of participation in the task, there was a significant interaction between Sex and Age Class (Table. 5), with adult males being significantly less likely to participate than juvenile males (β = -1.83, p = 0.0002), while in this model age class did not influence female participation (β = -0.06, p = 0.83) – note that this may be due to the reduced sample used for this analysis, which could only include individuals who participated at least once in the task. The variable of interest in this model, previous success, had a significant influence on the likelihood of participation (β = 0.37, p < 0.0001, see Figure. 6), with individuals being more likely to participate the more rewards they had received the last time they participated.

Table. 5: Results of a GLMM predicting the likelihood of participation by individuals per session in the task in the wild population, including the variable of interest: Previous Reward Count.

Effect	**Estimate**	**Wald 95% confidence interval**	***p*-value**
Intercept	-0.74	-1.67; 0.18	
Age Class (Adult)	-0.06	-0.50; 0.62	0.831
Sex (Male)	0.67	-0.15; 1.49	0.111
Previous Reward Count (z-transformed)	0.37	0.27; 0.47	< 0.0001
Group (Baie Dankie)	-0.77	-1.71; 0.17	0.110
Group (Kubu)	-0.50	-1.58; 0.58	0.365
Group (Noha)	-0.31	-1.23; 0.62	0.515
Session Duration (z-transformed)	0.40	0.32; 0.48	< 0.0001
Interaction: Age Class x Sex	-1.83	-2.79; -0.86	0.0002

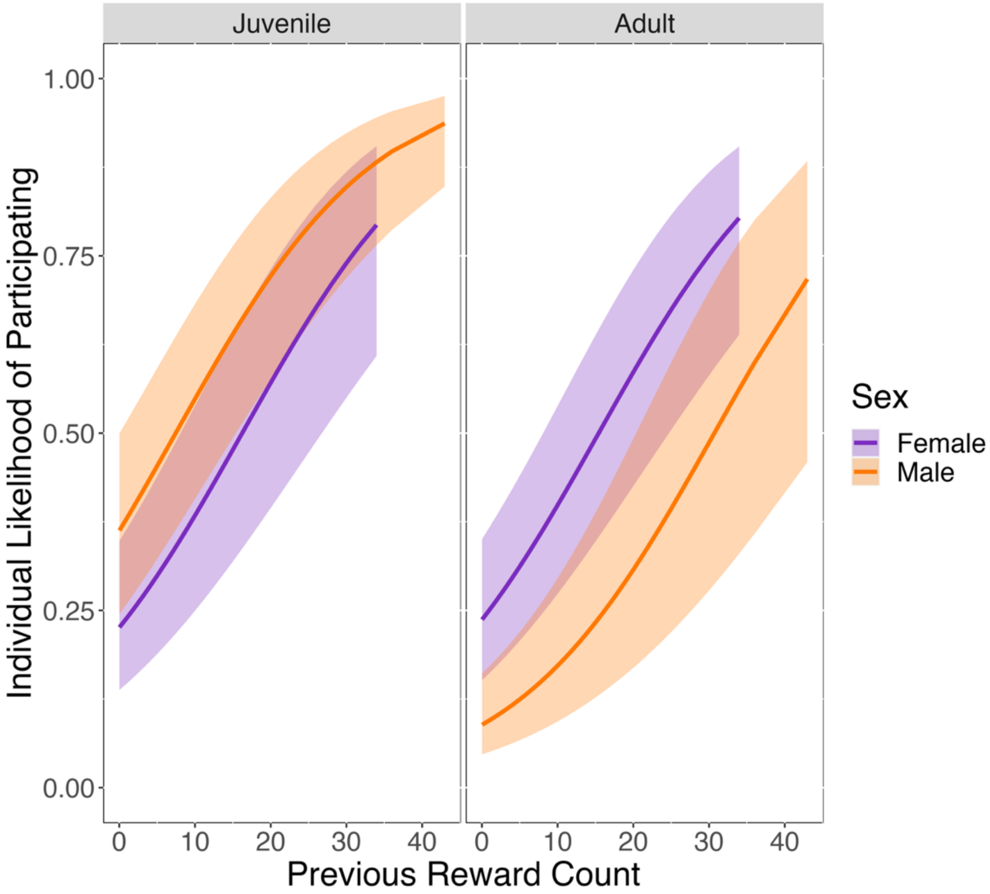


Figure. 6. Model predictions (estimated marginal means) of the effect of the number of Previous Rewards on the likelihood of participation in the task. The solid line shows the prediction for each Sex and Age Class, with shaded ribbons showing the 95% confidence interval.

3.5 Analysis 5: Trials required to pass Task 3

The full model (Analysis 5) analysing the number of attempts individuals required to pass Task 3 was not a better fit to the data than a null model containing only the random effect structure (χ^2 = 0.46, p = 0.50; see Table. S6 for full model output). Context had no impact upon the number of attempts an individual made before reaching criterion (Figure. 7; see Table. S6 for full model output).

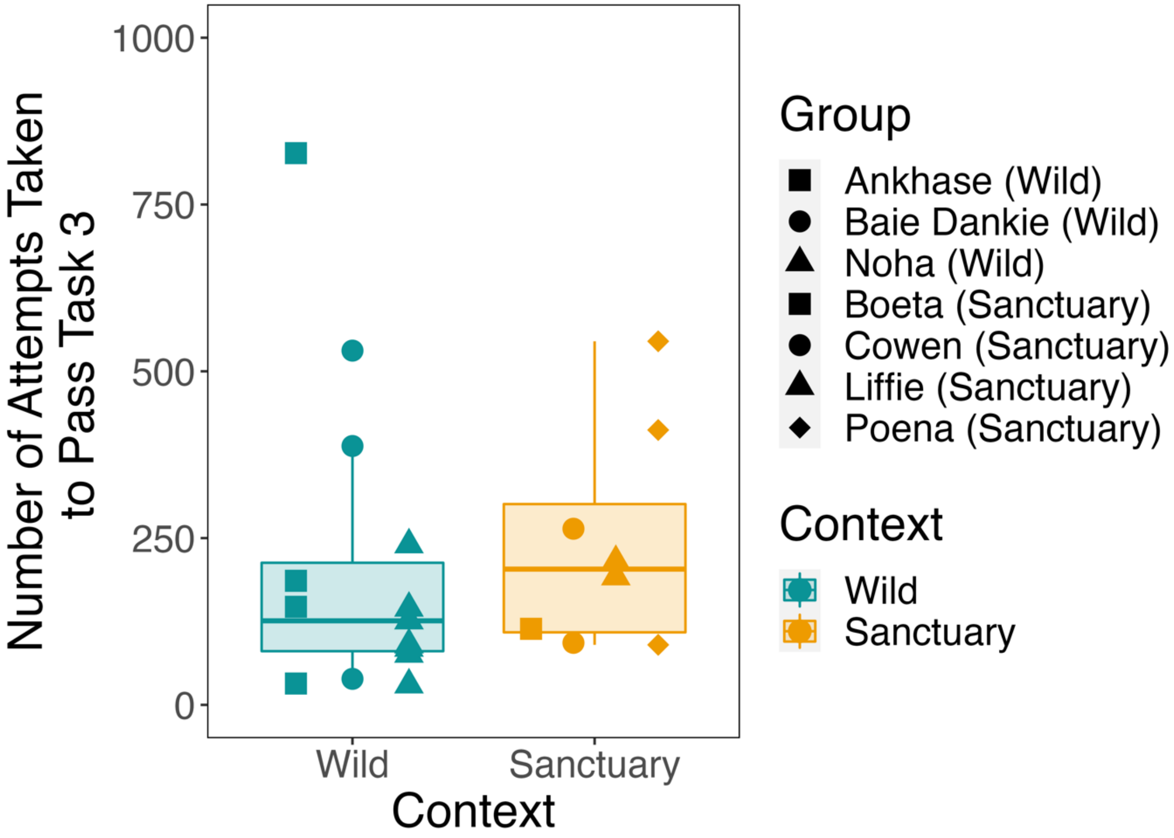


Figure. 7. The number of attempts made by individuals prior to reaching criterion on Task 2. Points show the number of attempts made by each individual, coloured by Context, with shape indicating Group membership. Boxplots show the median in a solid line, first and third quartiles at the upper and lower box edges, and whiskers show the largest and smallest values at 1.5 times the interquartile range of the distribution of observations for wild and sanctuary contexts.

4. Discussion

4.1 The influence of context on participation

In this study, we compared the participation rates of wild and sanctuary-housed vervet monkeys when offered a touchscreen device displaying various cognitive tasks. According to the free time hypothesis (Kummer & Goodall, 1985), we expected different rates of participation between sanctuary and wild vervet populations. Our results supported our hypothesis; participation level was influenced by environment. Captive individuals were significantly more likely to interact with the touchscreen than their wild conspecifics. This result supports the free time hypothesis, which would predict higher rates of participation in captive vervet monkeys which have more time and energy to spend interacting with experiments (Kummer & Goodall, 1985). Conversely, wild individuals may have had less free time to interact with the touchscreen due to the distraction of necessary activities such as foraging or being vigilant towards predators. It should be noted that group sizes were quite disparate between the wild and sanctuary groups tested in this study (see Table. S3), with three of the wild groups consistently containing more individuals than any of the sanctuary groups. It is therefore possible that group size influenced individuals' access to the task, with individuals in sanctuary groups having greater opportunities to interact due smaller group sizes resulting in reduced competition.

Despite significant differences in their likelihood of participation, individuals which reached criterion in Task 3 (learning to reliably touch a blue square, displayed in different locations on the screen, in order to get a reward) in both the wild and sanctuary-housed contexts did so with no difference in the number of attempts required. This result allows us to conclude that any differences in methodology between the two different environments did not affect the amount of time required for individuals to learn the association between touching the blue square and receiving a food reward, and also indicates that individuals in both contexts interacted meaningfully with the task. This result is in line with the findings of Cauchoix et al. (2017), who found no differences in reversal-learning performance between great tits tested in the wild and captivity and appears to be counter to the argument that captive primates display a 'captivity effect' in their cognitive abilities (Forss et al., 2020). However, this task was primarily a training task designed to facilitate later testing with more complex problems and is therefore relatively simple. It is possible that any captivity effect, or other differences in cognitive performance between wild and sanctuary populations, may become apparent only when using more challenging tests of cognition.

4.2 Group differences in the wild population

Within the wild population, group membership significantly influenced individuals' likelihood of participating in the task. Individuals in Baie Dankie (the largest group, N = 57 - 65) and Kubu (the smallest group, N = 15 - 18) were less likely to participate in testing than those in Ankhase (a medium-sized group, N = 23 - 26). Individuals in Kubu also made fewer attempts than those in Ankhase, and individuals in both Baie Dankie and Kubu made fewer attempts than those in Noha (a medium-sized group, N = 32 - 40). It is possible that membership of a larger group suppressed participation in the case of monkeys in Baie Dankie, due to higher rates of competition. This may have allowed high ranking individuals to monopolise the touchscreen; the effect of rank on participation should be explored in future studies.

Individuals in the smallest group (Kubu) were also less likely to participate. This group was habituated in 2013, more recently than the other wild groups tested in the study, and additionally has previously been found to have a lower habituation index than the other groups tested (Forss et al., 2021). It is therefore possible that in this group, while inter-individual competition for the task was reduced due to the small group size, reduced habituation to humans suppressed participation. Levels of participation may also have been influenced by variation in individual levels of habituation, along with factors such as personality (Webster & Rutz, 2020). Different groups may also contain individuals with differing dominance styles and resource holding potential, potentially rendering monopolisation a greater issue in some groups than others (as has been suggested as an explanation for differing levels of social tolerance in neighbouring chimpanzee groups, Cronin et al., 2014).

While we believe testing multiple groups of wild individuals represents a crucial step forward in our understanding of the impact of social factors upon cognition and behaviour, our interpretation of any differences remains limited somewhat by sample size when it comes to pinpointing the cause of between-group differences, as the four groups tested here are likely to differ in a number of parameters, group size and habituation being only two. Future studies could begin to tease this apart both by more detailed examination of interactions at and around the task (which is outside the scope of the current paper), for example examining the number of individuals who approached the task but were outcompeted, and by incorporating parallel tests of social tolerance and habituation to quantify existing group differences.

4.3 Phenotypic traits influenced participation in the wild population

Although many studies have shown that juveniles are less neophobic than adults (Bergman & Kitchen, 2009; Biondi et al., 2010; Miller et al., 2015; Visalberghi et al., 2003), and therefore we expected juveniles to participate and interact with the touchscreen more frequently than adults, our findings regarding this were impacted by sex. Male juveniles were indeed more likely to participate than adult males, but female juveniles were less likely to participate than adult females. Vervet monkeys have a complex social system based on a linear hierarchy organised by matrilines. In our context, it is very likely that juveniles had to wait for the end of monopolization by the high-ranking adult females before interacting with the experiment. Nonetheless, male juveniles were significantly more likely to participate than adult males. When they reach sexual maturity, male vervets disperse from their natal group. When juvenile males approach this milestone, they become less central and more independent (Young et al., 2019). It is therefore possible that the age class effect seen in wild juvenile males in our study is driven by highly explorative older juveniles and high competition levels between juvenile males and other group members. Our sample size did not allow detailed exploration of age effects and competition, but future research should explore these possibilities.

Regarding sex differences, we found that adult females made more attempts at the touchscreen than males. One possible explanation for this can derive from physiological needs. Females, especially during the gestation and lactating period, need higher energy intake and there were females in our sample who were pregnant and had offspring during the period of the experiment. We also found that adult females participated more than males in the experiments. In our study population, it has been shown that females are often dominant over males and many groups have a female as the most dominant individual in the group (Hemelrijk et al., 2020). Therefore, our results could be explained by the fact that dominant adult females might have the greatest opportunity to monopolize and interact with the touchscreen.

Within this study, we found that the likelihood of participation increased with the number of rewards a monkey had received the last time they participated. Additionally, regardless of the length of time between experiments, monkeys in both the wild and captivity were motivated to participate again (see Supplemental Information: Effect of breaks in testing). Both these findings could influence the design of future studies.

While our study demonstrates that it is possible to conduct cognitive tests using touchscreen technology in the wild, some sampling biases are likely to apply (Webster & Rutz, 2020) which may impact the generalisability of results, particularly regarding self-selection according to personality and habituation. Our findings indicate that some age and sex classes (adult females and juvenile males) were more likely to participate than others, suggesting that future studies may need to engage in some selection of individuals to achieve balanced samples in this regard – we suggest a potential method to achieve this below.

4.4 Future directions

To increase the number of individuals who can interact with touchscreens presented in the wild, it would be useful in the future to integrate more advanced technological methods such as automatic facial recognition (Schofield et al., 2019) or individual radio frequency identification (RFID: Bridge et al., 2019; Fagot & Paleressompoulle, 2009). We note that fitting RFID tags would require sedation of the study subjects and therefore may not be appropriate in many cases (Soulsbury et al., 2020), but could be an option in populations in which individuals are already sedated to fit GPS collars as a standard protocol, rather than sedating animals for the sole purpose of fitting RFID tags. These methods would allow the touchscreen to automatically present the appropriate task according to the individual interacting, and would allow the process to be automatized, with the touchscreen remaining in place in the field for prolonged periods. This would not prevent monopolisation, and so might result in larger amounts of data but not necessarily larger sample sizes. Automatization would also potentially facilitate the presentation of multiple touchscreens in the field at the same time, which likely would reduce the impact of monopolisation upon participation. To further address monopolisation, individuals could also be trained to recognize a visual pattern on the screen indicating that it is their turn to interact with the task, with the screen blocked for all individuals except the target participant. This procedure could also be used to generate more balanced samples in terms of age and sex class (a technique successfully used with artificial foraging boxes by Borgeaud and Bshary, 2015). We found that across the four wild groups, the total number of individuals interacting per session was relatively similar regardless of group size (see Supplemental Information: Number of individuals participating per session in wild groups), and so methods to increase presentation time by automating aspects of the process may help to increase sample sizes.

Further research could also explore in more detail how social factors influence participation in experimental tasks. Our findings point towards potential roles for group size and resulting competition, and inter-individual tolerance or monopolisation by dominant individuals. These represent potential constraints that testing in social contexts may place upon cognitive testing of wild animals. However, it is also likely that social factors facilitate participation and interaction with novel objects such as the touchscreen, through processes such as social facilitation (Dindo et al., 2009; Forss et al., 2017; Miller et al., 2014). There is also the potential for social learning to influence interaction with the task, via local or stimulus enhancement, or more high-fidelity forms of social transmission. As adult females were key participants in our task, and are the preferred models for social learning in wild vervet monkeys (van de Waal et al., 2010; Bono et al., 2018), the presence of adult females interacting with the task may well facilitate participation by other age sex classes in this species.

We believe that touchscreen testing with wild populations has the potential to provide a step forwards in studying non-human cognition. However, the potential ethical implications of this type of research must be carefully considered (Gruber, 2022). Like other types of field experiment, providing touchscreens for testing animals in their natural habitat removes the need to bring animals into captivity for testing, opening up the possibility of testing animals for which capturing would be unethical. This benefit aside, it is unlikely that touchscreen testing will be appropriate in all situations. The current set-up requires the relatively close presence of an experimenter, and food rewards are provided. The possibility of individuals forming an association between humans and food rewards may be dangerous in some species (for example, the great apes), and provisioning can carry risks (Fedigan, 2010). Exposure to human artefacts in the form of screens may also be considered unacceptable for some species (though we note that video demonstrations have previously been shown to wild primates (e.g. Gunhold et al., 2014). The population of monkeys tested in the current paper do not live in close proximity to humans, and therefore the risk of habituation to the touchscreen spilling over into increased attempts to interact with screens in other contexts is limited, but this should be considered if testing urban populations, for example. Additionally, the potential for exposure to the touchscreen to alter the natural behavioural repertoire of the subjects should be considered. Vervet monkeys are not endangered, and only a subset of groups resident at the IVP were included in touchscreen testing. However, for endangered species in which the natural behavioural repertoire must be carefully conserved, exposure to the touchscreen and other artificial experimental tasks may not be appropriate.

5. Conclusion

This study explored rates of participation at a novel touchscreen task in both wild and sanctuary-housed vervet monkeys. While participation rates were higher in sanctuary monkeys, in line with the ‘free time’ hypothesis, performance as measured by the number of trials taken to reach criterion in a task was the same across both contexts. Age and sex differences in participation of wild monkeys were observed, which may reflect different levels of neophobia and motivation between juveniles and adults and males and females, as well as the ability to compete for access to and monopolise the touchscreen. The study demonstrates that touchscreen technology can be deployed successfully in a wild primate population, and that while levels of participation may differ, results comparable to the performance of captive populations can be achieved. This opens the door for comparative studies examining the ways in which cognitive abilities may differ between wild and captive primate populations and offers the opportunity to validate results from captive studies in a wild population using identical methodology.

Acknowledgements

This study was supported by the Swiss National Science Foundation (PP03P3_170624 and PP00P3_198913) and the Branco Weiss Fellowship—Society in Science granted to Erica van de Waal. We are grateful to the van der Walt family for permission to conduct the study at Mawana game reserve and Sandy Cronk, owner of the rehabilitation centre for permission to conduct the study at W. A. T. C. H. We thank Ezemvelo KZN Wildlife who gave us permission to conduct our research on vervet monkeys in South Africa. We are also grateful to M. Henshall for managing the Inkawu Vervet Project and his help in the data collection. We thank all the team from the IVP for their support and help in data collection, with a special thanks to T. Henshall, M. German, and S. Glosenger-Thrasher, who provided great help in carrying out the experiments. We are grateful to V. Schmitt for her help with the touchscreen procedure and for her participation in the design of the study. We thank students from the EPFL (École Polytechnique Féderale de Lausanne) for writing the test code. Finally, we are grateful to the reviewers and editors for their constructive comments.

Conflict of interest

The authors have no conflict of interest to declare.

Author contributions

T. Mohr participated in the design of the study, collected field data, compiled the dataset and drafted the manuscript. E. van de Waal coordinates the research at IVP in South Africa, designed the study, financed the study and corrected the manuscript. R. A. Harrison conducted the data analysis, drafted and corrected the manuscript. All authors gave final approval for publication.

Data availability statement

All relevant data and analysis code are available at https://osf.io/p2xgq/?view_only=96c8ae0fe4e047b5bffb70724fcc554a

References

ASAB/ABS. (2020). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, *159*, I–XI. https://doi.org/10.1016/j.anbehav.2019.11.002.

Ashton, B. J., Thornton, A., & Ridley, A. R. (2018). An intraspecific appraisal of the social intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170288. https://doi.org/10.1098/rstb.2017.0288.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). *Fitting Linear Mixed-Effects Models using lme4* (arXiv:1406.5823). arXiv. https://doi.org/10.48550/arXiv.1406.5823.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., & Grothendieck, G. (2011). Package 'lme4'. *Linear Mixed-Effects Models Using S4 Classes. R Package Version*, *1*(6).

Bean, A. (1999). Ecology of sex differences in great ape foraging. In P. C. Lee (Ed.), *Comparative Primate Socioecology* (1st ed., pp. 339–362). Cambridge University Press. https://doi.org/10.1017/CBO9780511542466.017.

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

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

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

Bono, A. E. J., Whiten, A., van Schaik, C., Krützen, M., Eichenberger, F., Schnider, A., & van de Waal, E. (2018). Payoff- and Sex-Biased Social Learning Interact in a Wild Primate Population. *Current Biology*, *28*(17), 2800-2805.e4. https://doi.org/10.1016/j.cub.2018.06.015.

Borgeaud, C., & Bshary, R. (2015). Wild Vervet Monkeys Trade Tolerance and Specific Coalitionary Support for Grooming in Experimentally Induced Conflicts. *Current Biology*, *25*(22), 3011–3016. https://doi.org/10.1016/j.cub.2015.10.016.

Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. *Animal Behaviour*, *136*, 1–12. https://doi.org/10.1016/j.anbehav.2017.11.025.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357.

Bridge, E. S., Wilhelm, J., Pandit, M. M., Moreno, A., Curry, C. M., Pearson, T. D., Proppe, D. S., Holwerda, C., Eadie, J. M., Stair, T. F., Olson, A. C., Lyon, B. E., Branch, C. L., Pitera, A. M., Kozlovsky, D., Sonnenberg, B. R., Pravosudov, V. V., & Ruyle, J. E. (2019). An Arduino-Based RFID Platform for Animal Research. *Frontiers in Ecology and Evolution*, *7*. https://www.frontiersin.org/articles/10.3389/fevo.2019.00257.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/ RJ-2017-066.

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. *Nature Communications*, *11*(1), 459. https://doi.org/10.1038/s41467-019-14209-8.

Cauchoix, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field: Comparison of reversal learning performance in captive and wild passerines. *Scientific Reports*, *7*(1), 1–10. https://doi.org/10.1038/s41598-017-13179-5.

Cole, E. F., Morand-Ferron, J., Hinks, A. E., & Quinn, J. L. (2012). Cognitive Ability Influences Reproductive Life History Variation in the Wild. *Current Biology*, *22*(19), 1808–1812. https://doi.org/10.1016/j.cub.2012.07.051.

Cronin, K. A., van Leeuwen, E. J. C., Vreeman, V., & Haun, D. B. M. (2014). Population-level variability in the social climates of four chimpanzee societies. *Evolution and Human Behavior*, *35*(5), 389–396. https://doi.org/10.1016/j.evolhumbehav.2014.05.004.

Damerius, L. A., Forss, S. I. F., Kosonen, Z. K., Willems, E. P., Burkart, J. M., Call, J., Galdikas, B. M., Liebal, K., Haun, D., & van Schaik, C. P. (2017). Orientation toward humans predicts cognitive performance in orang-utans. *Scientific Reports*, *7*(1), 1–12.

Dindo, M., Whiten, A., & de Waal, F. B. M. (2009). Social facilitation of exploratory foraging behavior in capuchin monkeys (Cebus apella). *American Journal of Primatology*, *71*(5), 419–426. https://doi.org/10.1002/ajp.20669.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8.

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology*, *38*(2), 220–235.

Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior Research Methods*, *41*(2), 396–404. https://doi.org/10.3758/BRM.41.2.396.

Fairbanks, L. A., & McGuire, M. T. (1993). Maternal protectiveness and response to the unfamiliar in vervet monkeys. *American Journal of Primatology*, *30*(2), 119–129. https://doi.org/10.1002/ajp.1350300204.

Fedigan, L. M. (2010). Ethical issues faced by field primatologists: Asking the relevant questions. *American Journal of Primatology*, *72*(9), 754–771. https://doi.org/10.1002/ajp.20814

Forss, S. I. F., Koski, S. E., & van Schaik, C. P. (2017). Explaining the Paradox of Neophobic Explorers: The Social Information Hypothesis. *International Journal of Primatology*, *38*(5), 799–822. https://doi.org/10.1007/s10764-017-9984-7.

Forss, S. I. F., Motes-Rodrigo, A., Dongre, P., Mohr, T., & van de Waal, E. (2022). Captivity and habituation to humans raise curiosity in vervet monkeys. *Animal Cognition*, *25*(3), 671–682.

Forss, S. I. F., Motes-Rodrigo, A., Hrubesch, C., & Tennie, C. (2020). Chimpanzees'(Pan troglodytes) problem-solving skills are influenced by housing facility and captive care duration. *PeerJ*, *8*, e10263.

Forss, S. I. F., Schuppli, C., Haiden, D., Zweifel, N., & van Schaik, C. P. (2015). Contrasting responses to novelty by wild and captive orangutans: Novelty Response in Orangutans. *American Journal of Primatology*, *77*(10), 1109–1121. https://doi.org/10.1002/ajp.22445.

Gareta García, M., Lemieux, D., & Bshary, R. (2021). Factors affecting tolerance persistence after grooming interactions in wild female vervet monkeys, Chlorocebus pygerythrus. *Animal Behaviour*, *177*, 135–145. https://doi.org/10.1016/j.anbehav.2021.04.025.

Gruber, T. (2022). An ethical assessment of the use of old and new methods to study sociality in wild animals. *Methods in Ecology and Evolution*, *n/a*(n/a). https://doi.org/10.1111/2041-210X.13988.

Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates opportunities for chimpanzee tool use. *Behavioral Ecology*, *30*(4), 1136–1144.

Gunhold, T., Whiten, A., & Bugnyar, T. (2014). Video demonstrations seed alternative problem-solving techniques in wild common marmosets. *Biology Letters*, *10*(9), 20140439. https://doi.org/10.1098/rsbl.2014.0439

Harrison, R. A., Mohr, T., & van de Waal, E. (2022). Data from: Lab cognition going wild: Implementing a new portable touchscreen system in vervet monkeys. *Open Science Framework DIGITAL repository*. https://doi.org/10.17605/ OSF.IO/P2XGQ.

Harrison, R. A., & van de Waal, E. (2022). The unique potential of field research to understand primate social learning and cognition. *Current Opinion in Behavioral Sciences*, *45*, 101132.

Healy, S. D., & Hurly, T. A. (2013). What hummingbirds can tell us about cognition in the wild *Comparative Cognition & Behavior Reviews*, *8*,13–28. https://doi.org/10.3819/ccbr.2013.80002.

Hemelrijk, C. K., Wubs, M., Gort, G., Botting, J., & van de Waal, E. (2020). Dynamics of Intersexual Dominance and Adult Sex- Ratio in Wild Vervet Monkeys. *Frontiers in Psychology*, *11*. https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00839.

Hopper, L. M. (2017). Cognitive research in zoos. *Current Opinion in Behavioral Sciences*, *16*, 100–110.

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, *17*(23), R1004–R1005.

Kawai, N., & Matsuzawa, T. (2000). Numerical memory span in a chimpanzee. *Nature*, *403*(6765), 39–40.

Kendal, R., Coe, R., & Laland, K. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *66*(2), 167–188.

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

Kumpan, L. T., Smeltzer, E. A., & Teichroeb, J. A. (2020). Animal cognition in the field: Performance of wild vervet monkeys (Chlorocebus pygerythrus) on a Reversal Learning Task. *Animal Cognition*, *23*(3), 523–534.

Leinwand, J. G., Huskisson, S. M., Egelkamp, C. L., & Hopper, L. M. (2020). Within-and between-species variation in the responses of three primate species to a touchscreen gambling task. *Learning and Motivation*, *71*, 101635.

Li, M. F., Arseneau-Robar, T. J. M., Smeltzer, E. A., & Teichroeb, J. A. (2021). Be early or be tolerated: Vervet monkey, Chlorocebus pygerythrus, foraging strategies in a dispersed resource. *Animal Behaviour*, *176*, 1–15.

Martin, C. F., Muramatsu, A., & Matsuzawa, T. (2022). Apex and ApeTouch: Development of a Portable Touchscreen System and Software for Primates at Zoos. *Animals*, *12*(13), 1660.

Martina, C., Cowlishaw, G., & Carter, A. J. (2021). Individual differences in task participation in wild chacma baboons. *Animal Behaviour*, *172*, 73–91.

Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. *Chimpanzee Cultures*, 351–370.

McCune, K. B., Jablonski, P., Lee, S., & Ha, R. R. (2019). Captive jays exhibit reduced problem-solving performance compared to wild conspecifics. *Royal Society Open Science*, *6*(1), 181311.

Mertz, J., Surreault, A., van de Waal, E., & Botting, J. (2019). Primates are living links to our past: The contribution of comparative studies with wild vervet monkeys to the field of social cognition. *Cortex*, *118*, 65–81. https://doi.org/10.1016/j.cortex.2019.03.007.

Miller, R., Bugnyar, T., Pölzl, K., & Schwab, C. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology*, *69*(7), 1209–1220. https://doi.org/10.1007/s00265-015-1935-8.

Miller, R., Schiestl, M., Whiten, A., Schwab, C., & Bugnyar, T. (2014). Tolerance and Social Facilitation in the Foraging Behaviour of Free-Ranging Crows (Corvus corone corone; C. c. Cornix). *Ethology*, *120*(12), 1248–1255. https://doi.org/10.1111/eth.12298.

Morand-Ferron, J. (2017). Why learn? The adaptive value of associative learning in wild populations. *Current Opinion in Behavioral Sciences*, *16*, 73–79.

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: A review of practical and conceptual challenges. *Biological Reviews*, *91*(2), 367–389.

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: Associative learning in wild great tits. *PloS One*, *10*(8), e0133821.

Paula, J. R., Baptista, M., Carvalho, F., Repolho, T., Bshary, R., & Rosa, R. (2019). The past, present and future of cleaner fish cognitive performance as a function of CO2 levels. *Biology Letters*, *15*(12), 20190618. https://doi.org/10.1098/rsbl.2019.0618.

Pokorny, J. J., & de Waal, F. B. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences*, *106*(51), 21539–21543.

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

R Core Team. (2020). *R: A Language and Environment for Statistical Computing.*

Raine, N. E., & Chittka, L. (2008). The correlation of learning speed and natural foraging success in bumble-bees. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1636), 803–808.

RStudio Team. (2020). *RStudio: Integrated Development Environment for R.* www.rstudio.com.

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., Wismer, S., Stoinski, T., Brosnan, S. F., & Bshary, R. (2012). Adult Cleaner Wrasse Outperform Capuchin Monkeys, Chimpanzees and Orang-utans in a Complex Foraging Task Derived from Cleaner – Client Reef Fish Cooperation. *PLOS ONE*, *7*(11), e49068. https://doi.org/10.1371/journal.pone.0049068.

Schmitt, V. (2018). Implementing new portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. *bioRxiv*, 316042. https://doi.org/10.1101/316042.

Schmitt, V. (2019). Implementing portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. *Journal of Zoo and Aquarium Research*, *7*(2), 50–58. https://doi.org/10.19227/jzar.v7i2.314.

Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., & Carvalho, S. (2019). Chimpanzee face recognition from videos in the wild using deep learning. *Science Advances*, *5*(9), eaaw0736. https://doi.org/10.1126/sciadv.aaw0736.

Seferta, A., Guay, P., Marzinotto, E., & Lefebvre, L. (2001). Learning differences between feral pigeons and zenaida doves: The role of neophobia and human proximity. *Ethology*, *107*(4), 281–293.

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal Behaviour*, *61*(2), 277–286. https://doi.org/10.1006/anbe.2000.1606.

Soulsbury, C. D., Gray, H. E., Smith, L. M., Braithwaite, V., Cotter, S. C., Elwood, R. W., Wilkinson, A., & Collins, L. M. (2020). The welfare and ethics of research involving wild animals: A primer. *Methods in Ecology and Evolution*, *11*(10), 1164–1181. https://doi.org/10.1111/2041-210X.13435.

Szabo, B., Valencia-Aguilar, A., Damas-Moreira, I., & Ringler, E. (2022). Wild cognition–linking form and function of cognitive abilities within a natural context. *Current Opinion in Behavioral Sciences*, *44*,101115. https://doi.org/10.1016/j.cobeha.2022.101115.

Therneau, T. M. (2015). Package ‘coxme’. *R Package Version*, *2*(5).

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468.

van de Waal, E., Claidière, N., & Whiten, A. (2013). Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. *Animal Behaviour*, *85*(1), 71–76. https://doi.org/10.1016/j.anbehav.2012.10.008.

van de Waal, E., Claidière, N., & Whiten, A. (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. *Animal Cognition*, *18*(3), 617–627. https://doi.org/10.1007/s10071-014-0830-4

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1691), 2105–2111. https://doi.org/10.1098/rspb.2009.2260.

van de Waal, E., & Whiten, A. (2012). Spontaneous Emergence, Imitation and Spread of Alternative Foraging Techniques among Groups of Vervet Monkeys. *PLOS ONE*, *7*(10), e47008. https://doi.org/10.1371/journal.pone.0047008.

van Horik, J. O., Langley, E. J., Whiteside, M. A., & Madden, J. R. (2017). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural Processes*, *134*, 22–30.

Visalberghi, E., Janson, C. H., & Agostini, I. (2003). Response Toward Novel Foods and Novel Objects in Wild Cebus apella. *International Journal of Primatology*, *24*(3), 653–675. https://doi.org/10.1023/A:1023700800113.

Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*(7812), 337–340. https://doi.org/10.1038/d41586-020-01751-5.

Woolverton, W., Ator, N., Beardsley, P., & Carroll, M. E. (1989). Effects of environmental conditions on the psychological well-being of primates: A review of the literature. *Life Sciences*, *44*(14), 901–917.

Young, C., McFarland, R., Ganswindt, A., Young, M. M. I., Barrett, L., & Henzi, S. P. (2019). Male residency and dispersal triggers in a seasonal breeder with influential females. *Animal Behaviour*, *154*, 29–37. https://doi.org/10.1016/j.anbehav.2019.06.010.

Title Chapter 3:

"Mind Games: Unraveling the Puzzle of Manual Lateralisation and Stimuli Dimensionality in Vervet Monkeys

Tecla Mohr [a, b, c] *, Rachel A. Harrison[b, c], Charlotte Canteloup [a, b, c, d] & Erica van de Waal [a, b, c, e]

[a] Inkawu Vervet Project, Mawana Game Reserve, South Africa

[b] Department of Ecology & Evolution, University of Lausanne, Lausanne, Switzerland

[c]The Sense Innovation and Research Center, Lausanne and Sion, Switzerland

[d]Laboratory of Cognitive & Adaptive Neurosciences, UMR 7364, CNRS, University of Strasbourg, France

[e]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal,

Pietermaritzburg, South Africa.

*Corresponding author: mohr.tecla@gmail.com (TM)

Abstract

Despite improvements in the development of new automated devices in the wild, most cognitive experiments using touch screens have been conducted on captive animals. In this study, we explored the cognitive abilities of wild and sanctuary vervet monkeys by utilizing touchscreens. Initially, the study focused on sanctuary vervet monkeys in order to determine whether there was a difference in the ability of sanctuary monkeys to use 2D and 3D stimuli. The findings revealed that both sanctuary and wild vervet monkeys were capable of learning and completing Match-to-Sample and Reversal learning tasks on touchscreens. Moreover, the study revealed that sanctuary monkeys outperformed wild monkeys in the Match-to-Sample task. Furthermore, we analysed video recordings to determine whether the choice of body part used to touch the screen and the location of the correct stimulus impacted performance. The results indicated that individuals who used their muzzle tended to perform better than those using their left hands. When we looked at the ability to reverse the association, there was no difference between populations. This study highlights the importance of utilizing similar methods to compare the cognitive abilities of captive and wild animals.

1. Introduction

1.1 Wild vs. Sanctuary cognitive experiments

In recent years, there has been an increasing trend towards conducting cognitive experiments on a range of species in their natural habitats. While wild animals must cope with the challenges posed by their natural environments, captive individuals are often subjected to controlled environments that may lack the necessary environmental stimulation for them to develop cognitively. Studies on animal cognition are typically carried out in controlled laboratory environments, allowing researchers to control external factors like food availability, lighting conditions, and social surroundings (MacDonald & Ritvo, 2016). Confined animals are often tested to assess their behavioural adaptability, memory, and discernment skills. Researchers have conducted studies on the navigation and spatial problem-solving abilities of mice (Wolff et al., 2004), as well as the tool-use abilities of primates and crows in obtaining food (See review Seed and Byrne, 2010). They have also explored memory in birds using associative learning tasks and taught numerical discrimination abilities (Agrillo et al., 2017, Boysen and Hallberg, 2000). Additionally, animals have been tested for their social skills of learning and communication in monitored environments. These findings are often considered pertinent to cognition and behaviour in wild animal populations (De Petrillo et al., 2022). Over the past decade, there has been an increasing requirement for cognitive experiments to compare the cognitive abilities of various species that live in different environments. The study of both captive and wild animals increases our comprehension of their capacity for problem-solving, learning mechanisms, and adaptability. Two hypotheses have been proposed: 1) The resemblance between the performances of wild and captive animals may indicate an absence of cognitive distinctions between the two groups, and 2) The differences observed could be attributed to the presence of methodological drawbacks or real variations between the populations. The experiments focused on investigating associative learning in wild great tits (*Parus major*, Morand-Ferron et al., 2015), chacma baboons (*Papio ursinus*, Martina et al., 2021), and problem-solving skills in spotted hyenas (*Crocuta crocuta*, Benson Amram et al., 2013), had the objective to assess the cognitive abilities of captive animals and compare them with those of animals in their respective natural habitats. To enhance our capacity to monitor and examine the behaviour and cognition of wild and captive individuals, experts have created sophisticated technologies such as radio frequency identification (Aguzzi et al., 2011), eye tracking (Ryan et al., 2019), and automated systems that enable animals to undergo testing without human presence (Joël Fagot & Paleressompoulle, 2009), some of these advances have been discussed in previous work (Evans et al., 2013; Martin et al., 2022; Rutz & Hays, 2009). This abundance of innovation has enabled researchers to investigate semi-free ranging and wild animals, from mechanized puzzle boxes in vervets and great tits (Bono et al., 2018; Borgeaud et al., 2017; Morand-Ferron et al., 2015) to sophisticated systems such as battery-powered touchscreens in primates showing stimuli on the screen (Joël Fagot & Bonté, 2010; Hopper et al., 2019; Harrison et al., 2023). While there has been extensive research on animal cognition, only a handful of studies in birds (Cauchoix et al., 2017; Gajdon et al., 2004; Morand-Ferron, Cole, et al., 2011; Morand-Ferron et al., 2004), hyenas (Benson Amram et al., 2013), elephants (*Loxodonta africana and Elephas maximus* , Chevalier-Skolnikoff & Liska, 1993), and vervet monkeys (van de Waal et al., 2013) have succeeded in comparing the performance of captive and wild animals. Captive individuals outperformed wild individuals in almost all of these experiments. The only exception was Cauchoix et al. (2017), where wild and captive great tits performed similarly in a sequential spatial Reversal Learning Task using operant boxes. Throughout the experiment, participants were given the opportunity to choose between two stimuli, left or right, with the condition that the correct colour was chosen to receive a reward.

1.2 Transfer from 3D to 2D methodology

Historically many cognitive studies have been conducted using 3D stimuli which involved real world objects. 3D stimuli have been used to understand how animals interact with their environments and solve problems. From the development of advanced technology researchers have presented animals with 2D stimuli, two-dimensional images, typically displayed on flat surfaces such as computer screens. Thanks to the use of an automatic device for presenting stimuli, the transition from 3D to 2D has enabled researchers to establish better-controlled experimental conditions and a standardised approach to presenting stimuli in repeatable experiments. As animals have a different ability to associate real objects than 2D images (Cole & Honig, 1994; Fagot, 2013) and appear to pay more visual attention to real objects (Mustafar et al., 2015), most cognitive tests have been conducted using 3D stimuli. Horses recognised conspecifics based on specific cues, such as social cues conveyed by a near-realistic 3D model but not a drawing (Hanggi, 2001). Approach and sniffing behaviours are also associated with exploration meaning that using explorative responses as outcome measures is not specific to image recognition alone and could result from other motivations, such as gathering novel information. To not limit the need of animals to acquire explorative responses some researchers, for example have tested animals such as pigeons (Blough, 1959) horses (Hanggi, 2001) and guinea baboons (Fagot, 2010) in their ability to discriminate objects first and images in a second time.

1.3 Match-to-Sample tasks

One frequently used assessment for exploring animal behaviour and cognition is the delay Match-to-Sample test (MTS), which was developed by Hunter in 1948 (Hunter, 1948). This challenging cognitive assessment requires both working memory and conceptual comprehension. The MTS exercise requires participants to identify a matching sample stimulus with a test stimulus (Anderson & Colombo, 2022). The matching stimulus is rewarded while a presented alternative is not, following a predetermined rule. This test has been employed to assess short-term memory in a variety of animals, including Japanese macaques (*Macaca fuscata*), Guinea baboons (*Papio papio*, Maugard et al., 2013), tufted capuchin monkeys (*Cebus apella*, Truppa et al., 2011), chimpanzees (Grilly, 1975), rats (*Rattus norvegicus domestica*, Wallace et al., 1980), pigeons (Columba livia *domestica,* Zentall & Smith, 2016), cleaner fish (*Labroides dimidiatus*, Aellen et al., 2022), and zebrafish (*Danio rerio*, Bloch et al., 2019; See review Lind et al., 2015).

1.4 Lateralisation influence on performance

When animals solve problems, they may display a preference for using a particular hand or paw, much like handedness in humans, which involves motor skills. This is commonly known as "lateralisation" or "laterality" in animals. Studies in different animals such as cats (*felis catus*, Fabre-Thorpe et al., 1993, Isparta et al. 2020), yellow-bellied tits (*Pardaliparus venustulus*, Yin et al., 2023), dogs (*Canis familiaris*) and elephants (Haakonsson and Semple, 2009; Lefeuvre et al., 2022), have demonstrated the role of lateralisation strength in promoting cognitive abilities. Some studies have proposed a correlation between hand preference in primates and the difficulty level of the presented task (Fagot 1991). Over the last decade, researchers have employed touchscreen technology to explore lateralisation in animals and investigate whether they have a preference for interacting with a specific side (left or right) of the touchscreen. Do animals that exhibit lateralisation have a higher or lower likelihood of switching preferences when faced with a new task?

1.5 Reversal learning tasks

The Reversal Learning Task (RLT) is widely used to examine animals' ability to display cognitive flexibility. This task gauges flexibility by necessitating animals to reverse a prior association and match it with a new set of stimuli. Once they have learned this initial association, the task requires the animal to reverse it, indicating their ability to flexibly adapt their behaviour to new information. The study, carried out by

Degrande et al. (2022), examines the intricacies of animals' ability to comprehend a Reversal Learning Task. Numerous studies have been conducted to assess reversal abilities in captive rhesus macaques (Voytko, 1999), semi-reared Guinea baboons (Bonté et al., 2014), free-ranging great tits (Morand-Ferron et al., 2015), and wild habituated vervet monkeys (Kumpan et al., 2020). The findings of the study demonstrate the ability of wild vervet monkeys to reverse an association using 3D stimuli. Reversal learning tasks present valuable insights into how animals adapt to changing environmental conditions and solve problems they have previously learned.

1.6 Aim and hypotheses

The objective of our research was to evaluate the efficacy of touchscreens in gauging the cognitive capabilities of sanctuary vervet monkeys using 2D and 3D stimuli. To accomplish this, we administered a Match-to-Sample experiment and an associative Reversal Learning Task utilizing 2D and 3D stimuli. In the 2D experiment, the monkeys were required to accurately touch the appropriate stimulus on the screen, while in the 3D experiment, they had to lift objects to locate soaked corns. According to previous study (Mustafar et al., 2015), we predicted that the testing methodology would have an impact on task performance. We specifically predicted that sanctuary vervet monkeys would exhibit better performance with 3D stimuli as opposed to 2D stimuli (Mustafar et al. 2015). We first confirmed that the monkeys could associate 2D stimuli before conducting the MTS and RLT tasks on both wild and sanctuary vervet populations using touchscreens. Both populations were familiar with touchscreens, having previously been trained by Harrison et al. in 2023 to touch a blue square displayed on a white screen (Harrison et al., 2023). We hypothesized that sanctuary monkeys would perform better than their wild counterparts, which was attributed to the absence of predator distractions and the need to forage (according to the free time hypothesis, Kummer & Goodall 1965). Furthermore, the flexibility of both groups was assessed through a touch screen Reversal Learning Task. In the RLT, we used the same stimuli as in the MTS, but we switched the rewarded stimulus. In accordance with previous studies in free-ranging and captive great tits and vervet monkeys (Cauchoix et al., 2017, Kumpan 2020), we predicted similar performance in the RLT in wild and sanctuary vervet monkeys. At the individual level, we examined whether individual characteristics such as age and sex had an influence on performance in both cognitive tests, using only wild individuals, due to imbalanced ratios of individuals of the same sex and age at the sanctuary. Juveniles are known to be more exploratory and persistent than adults (Biondi et al., 2010; Martina et al., 2021; Morand-Ferron, Wu, et al., 2011). Based on our predictive analysis, we formulated a hypothesis that suggests a superior performance by juveniles in both tasks. The findings of McDowell's study indicate that female rhesus monkeys exhibited a lower level of distraction and committed fewer errors during a delay Match-to-Sample test (McDowell et al., 1960). In a delay Match-to-Sample experiment conducted by Grilly in 1975, comparable findings were obtained with chimpanzees (Grilly, 1975). The results indicated that female chimpanzees possessed superior matching abilities when compared to their male counterparts. Based on earlier research, as well as the greater involvement of females in touch screen usage observed by Harrison et al. (2023), we postulated that females would outperform males in solving MTS tasks. In addition, we predicted that there may be a correlation between performance and manual lateralisation. For hand preference in primates, there is evidence that primates such as baboons choose their hands according to the skill required by the task (Fagot & Vauclair, 1988). Vauclair et al. (1987) conducted an experiment to evaluate the proficiency of baboons in handling one-handed and two-handed food tasks using peanut butter spread on the ground and in a tube. Their findings indicated that baboons displayed a greater preference for their right hand in the two-handed task. Our project, on the other hand, did not involve a two-handed task but focused on presenting two stimuli on opposite sides of the screen and assessing the monkeys' ability to coordinate their responses accordingly. Our hypothesis was that the monkeys would have the ability to adapt their choices of which hand to use depending on the location of the correct stimulus (Vauclair & Fagot, 1987).

2. Material and methods

2.1 Study

Between February 2021 and February 2022, we collected data on three distinct groups of wild vervet monkeys (Ankhase, Baie Dankie and Noha). These groups were located in the Inkawu Vervet Project (IVP), situated within the Mawana Game Reserve in South Africa. Additionally, we also conducted a study on three sanctuary vervet monkey groups (Boeta, Cowen and Poena) at the Wild Animals Trauma Centre and Haven (W. A. T. C. H.) rehabilitation centre, in Kwazulu-Natal, South Africa.

2.2 Subjects

In 2010, the IVP began to follow four groups of wild vervet monkeys on a daily basis with the help of researchers and fieldwork. Each monkey was identified based on their unique physical features, such as scars, eye rings, and body shape. The wild groups consisted of adult males and females, juvenile males and females, and infants, as detailed in Table. 1. Females were considered adults when they either gave birth for the first time or reached five years of age, and males were considered adults when they dispersed from their birth group or reached five years of age. Juveniles were defined as individuals between four months of age (regardless of maternal dependency) and the age of adulthood, as previously defined. Numerous monkeys were tested, but only seven individuals successfully met the learning criterion to pass the MTS task. and only three passed for the Reversal Learning Task. Testing took place in the wild at sunrise, between 4:30 am and 8:00 am, near the monkeys' sleeping site.

Table. 1: Composition of wild (white) and sanctuary groups (grey) at the start of the experiment.

Context	**Group**	**Age Sex Class**	***Total Number***
Wild N = 100	Ankhase N = 21	Adult Female	8
		Adult Male	5
		Juvenile Female	3
		Juvenile Male	5
	Baie Dankie N = 48	Adult Female	*19*
		Adult Male	10
		Juvenile Female	9
		Juvenile Male	10
	Noha N = 31	Adult Female	10
		Adult Male	7
		Juvenile Female	7
		Juvenile Male	7
Sanctuary N = 33	Boeta N = 3	Adult Female	1
		Adult Male	2
		Juvenile Female	0
		Juvenile Male	0
	Cowen N = 12	Adult Female	2
		Adult Male	1
		Juvenile Female	1
		Juvenile Male	8
	Poena N = 18	Adult Female	3
		Adult Male	1
		Juvenile Female	4
		Juvenile Male	10

We conducted experiments on three groups of sanctuary vervet monkeys, including orphans, injured individuals, and those saved from roadsides or street markets. These groups were housed in large outdoor enclosures and had social groups of up to 25 individuals. Two groups had a mix of males and females of various ages, while the third group had only three adults – two males and one female. We conducted the MTS experiment on a population of 33 sanctuary monkeys within seven individuals passed the MTS task, while four individuals completed the RLT task. Testing was scheduled in the afternoon to avoid reflections on the touch screen due to the lack of shelter from the sun in the enclosures. Experiments at W. A. T. C. H. took place between 1 p.m. and 6 p.m. Monkeys had free access to water and food in the enclosures.

All monkeys tested had prior touchscreen training, completing basic associative tasks with a blue square on a white background (Harrison et al., 2023).

2.3 Material and procedure

In our project, we utilised the Zoo-based Animal-Computer-Interaction System (ZACI) shown in Figure 1A, previously used in experiments with vervet monkeys (Harrison et al. 2023). For a year, from February 2021 to February 2022, we conducted two tests per week on the monkeys. Each trial involved the presentation of a match stimulus (S+), followed by two simultaneous stimuli: a non-matching stimulus (S-) and a matching stimulus (S+), as detailed in Table. 2. The trials were conducted on a white background, displaying one or two symbols (as in Table. 2). Both wild and sanctuary populations received the same stimulus pairs, with each group receiving a distinct pair, resulting in three stimulus pairs (also listed in Table. 2). Each monkey participated in a maximum of 10 trials per day before being blocked from further participation with a black screen.

In Experiment 1, we tested the ability of three sanctuary groups (Boeta, Cowen and Poena) with a total of 30 individuals (7 adults and 23 juveniles, including 20 males and 10 females) to solve an associative learning task by transferring between 2D images on a touchscreen and 3D stimuli. We had to remove Boeta's group, three adult participants (two males and one female) from the study due to their failure to complete the experiment with 3D stimuli. The experiment was conducted outside the enclosures using two different methods. For the first method we used 3D stimuli, three sets of coloured cups and cones made of cardboard. One stimulus was placed on the left and one on the right of a metal trolley (Figure.

1B) to enable easy movement of the setup in case the monkeys selected the wrong stimulus or approached the setup after reaching the maximum of 10 trials. The positions of the S- and S+ (right and left) were randomly presented on each trial. The reward (one large or two small soaked corn kernels) was placed under the S+ and could be accessed by selecting the correct stimulus by lifting or knocking it over. If the monkey chose the wrong stimulus, the tray was immediately removed before they could access the second stimulus. After each trial, the two stimuli were removed and covered with cardboard. As some subjects had already finished the trial, the trolley was moved away from the fence, and corn was offered on the other side of the enclosure to distract them.

In our second experiment utilizing 2D stimuli, we adhered to the same methodology as the Match-to-Sample experiment detailed previously using 3D stimuli. To eliminate any potential influence from the procedure order, we randomized the order of the procedure between groups and the set of stimuli. Cowen's group began with 3D stimuli, while Poena's group started with 2D stimuli. Each session lasted a maximum of 10 trials. The experiment was deemed successful when the monkeys successfully completed the learning criterion of seven correct trials in three consecutive sessions of 10 trials, eight correct trials in two consecutive sessions, or nine correct trials in one session (learning criterion, Paula et al., 2019 and Salwiczek et al., 2012). Once the monkeys reached the learning criterion, we conducted the Reversal Learning Task with 2D stimuli by reversing the correct stimuli. We scheduled sessions twice a week in each enclosure. Unfortunately, due to time constraints, we were unable to continue the experiment with 3D stimuli in Boeta's group.

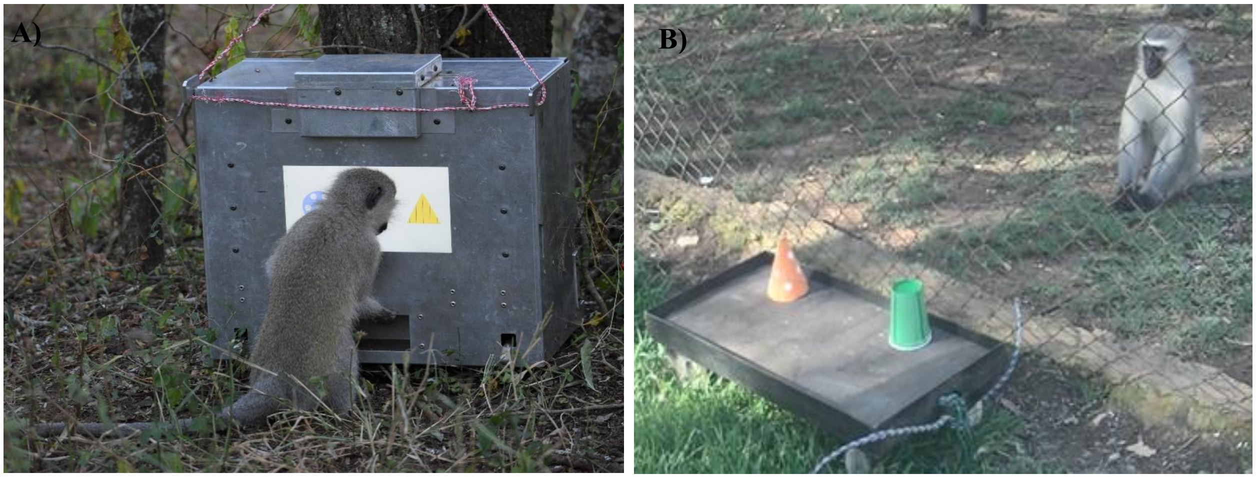


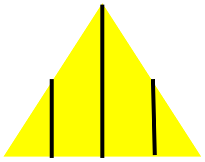
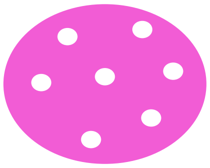
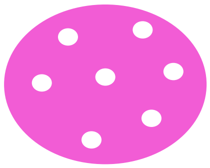
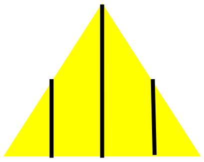
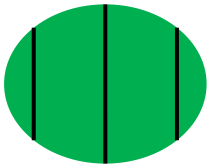
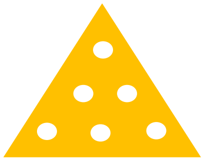
Figure. 1: Example of set up used during 3D experiment (A), Transfer experiment and (B). For the MTS and the RLT experiments using touchscreen, we showed simultaneously two stimuli, one the right and

left side of the screen. To be food rewarded sanctuary monkeys had to touch the correct stimulus. For the transfer experiment, we showed simultaneously two stimuli, one on the right side and one the left side of the tray. Below one of the stimuli we hided some corn as reward. To access it monkeys had to choose the correct stimulus by lifting or knocking over it. Copyright, Maxine Piron (A), Tecla Mohr (B).

2.4 Procedure: Match-to-Sample

During Experiment 2, we utilised a Match-to-Sample (MTS) approach to evaluate the cognitive abilities of wild and sanctuary vervet monkeys. Participants were presented with a matching sample stimulus on a white screen in the initial phase of the task. In the subsequent phase, a pair of stimuli consisting of one matching stimulus and one non-matching stimulus was displayed. Upon successfully matching the sample stimulus, the monkey was rewarded with three to four corn kernels dispensed from the food dispenser. The monkey passed the MTS task when they met the learning criterion described previously. We conducted sessions twice a week in both sanctuary and wild populations. To prevent monopolisation, each individual was limited to a maximum of 10 choices per session. For additional information, please refer to Supplementary data, Table. S1.

Table. 2: Three combinations of 2D and 3D stimuli used. Both stimuli were represented on the screen simultaneously, one on the right side and one on the left. The sample stimulus (SS) was shown at the beginning of each trial. Correct stimulus (S+) was rewarded by a few soaked corns.

	Correct Stimulus (SS/S+)	**Incorrect Stimulus (S-)**
Set 1 2D: Baie Dankie and Cowen 3D Poena		
Set 2 2D: Noha and Boeta 3D Cowen		
Set 3 2D: Ankhase and Poena		

2.5 Procedure: Effect of manual lateralisation on success task

During the touchscreen experiment, we collected additional data by recording all trials on video. For every Match-to-Sample trial, we noted the matching stimulus side (S+), the body part utilised for screen touch (right hand, left hand, or muzzle), and the touch accuracy.

2.6 Procedure: Reversal learning task

In the Reversal Learning Task (RLT) we assessed the capacity of sanctuary and wild vervet monkeys to forget one association and establish a new one. Initially, the monkeys were trained to associate two stimuli (Set 1, Set 2, or Set 3). After meeting the learning criterion in the Match-to-Sample study, the previously rewarded stimulus (S+) was replaced (as indicated in Table. 2), and the identical learning threshold was used.

2.7 Statistical analyses

We utilised R software (Team, 2022) to carry out statistical analysis and we opted for non-parametric tests due to the limited sample size. Out of the 17 sanctuary individuals, only four were able to meet the learning criterion in both the 2D and 3D stimuli of MTS and RLT. However, the sample size was inadequate to conduct a statistically significant analysis of testing performance in the RLT. As a result, we present a descriptive analysis of the primary observations and findings. For Analysis 1, we used Mann-Whitney U tests to test the impact of context (wild vs. sanctuary), age class (adult vs. juvenile), and sex (male vs. female) on the number of trials required to pass the MTS experiment.

Our research aimed to investigate whether lateralisation affects MTS performance. We collected and analysed data from 13 wild and nine sanctuary monkeys who participated in the MTS experiment at least once. We used a binomial GLMM test (analysis 2) to compare correct vs. incorrect trials as the outcome variable. Our predictor variables included context (wild vs. sanctuary), age class (adult vs. juvenile), sex (female vs. male), side of the correct stimulus (right vs. left), and body part used to touch the screen (right hand vs. left hand vs. muzzle), with individual as a random variable. Only individuals who met the criterion in the Match-to-Sample experiment (N = 14) were included in Analysis 2. To prepare for Analysis 3, we calculated the percentage of trials in which each animal used their right hand, left hand and muzzle (see Table. S1). We established a minimum criterion of 50% use for one body part to determine the body part preference. Three individuals who did not meet the 50% minimum for any body part used were excluded from the analysis. In Analysis 3, we employed a binomial GLMM with an interaction between side and preferred body part as predictor variables, and individual as a random variable.

To evaluate the influence of context, age class, and sex on performance in the Reversal Learning Task, we employed Mann-Whitney U tests (Analysis 4). The effect of age class on performance in the Reversal Learning Task was not feasible due to the learning criterion not being met by any juveniles. Moreover, we employed the Mann-Whitney test (Analysis 5) to compare the number of trials made by individuals in both the MTS and RLT tasks.

2.8 Ethical approved

Our study adhered to the ASAB/ABS Guidelines for the use of animals in research (ASAB/ABS, 2020) and was approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa. Ethical approval was not required by the authors' institutions.

3. Results

3.1 Analysis 1: Transfer experiment

Due to the small sample, we could not run any statistical analysis to compare the performance of individuals in a Match-to-Sample experiment using 2D vs. 3D stimuli. Table. 3 displays the results of 17 participants who completed the experiment with 3D stimuli, with a mean of 34.12 trials needed to reach criterion. Notably, adult female Lilly reached the criterion in only 11 trials, while juvenile male Tim required 54 trials. Only four of the 17 individuals completed the experiment using 2D and 3D stimuli. On average, these participants required 30 trials with 3D stimuli and 77.5 trials with 2D stimuli. Of the four who completed the experiment with 2D stimuli, juvenile male Fanjan was the fastest with 70 trials, while Gyzmo, Poena, and Cowen all required 80 trials. Two participants started the experiment with 2D stimuli but did not finish.

Table. 3: Represents the list of individuals who participated in the MTS task with the number of trials and touches used to associate 2D and 3D stimuli.

Individual	**Sex**	**Age class**	**Group**	**Nr of trials taken to pass MTS using 3D stimulus**	**Nr of trials taken to pass RLT using 3D stimulus**	**Nr of trials taken to pass MTS using 2D stimulus**	**Number of trials taken to pass RLT using 2D stimulus**	**Which methodology individuals start the experiment**
Fanjan	M	Juvenile	Poena	19	33	70	NA	3D

Gizmo	M	Juvenile	Poena	21	79	80	NA	2D
Poena	F	Adult	Poena	20	90	80	100	2D
Cowen	F	Juvenile	Cowen	44	NA	80	NA	3D
Alfie	M	Juvenile	Poena	33	81	NA	NA	3D
Brighteye	M	Adult	Poena	26	73	NA	NA	3D
Hugh	M	Juvenile	Poena	33	79	NA	NA	3D
Lilly	F	Adult	Poena	11	NA	NA	NA	3D
Minu	F	Juvenile	Poena	51	34	NA	NA	3D
Mo	M	Juvenile	Poena	40	43	NA	NA	3D
Rudolph	M	Juvenile	Poena	41	32	NA	NA	3D
Grace	F	Juvenile	Cowen	30	NA	NA	NA	3D
Jeff	M	Juvenile	Cowen	31	40	10 (not finished)	NA	3D
Milo	M	Juvenile	Cowen	36	NA	NA	NA	3D
Neelsie	M	Juvenile	Cowen	50	50	60 (not finished)	NA	3D
Tim	M	Juvenile	Cowen	54	NA	NA	NA	3D
Tony	M	Juvenile	Cowen	35	NA	NA	NA	3D

3.2 Analysis 2: Match-to-Sample

During this experiment, we collected data from six groups of monkeys. The study focused on 14 monkeys, seven from each context, who completed a Match-to-Sample task using 2D stimuli. The aim was to measure performance based on the number of trials it took to reach the learning criterion to pass MTS experiment. We employed Mann-Whitney U tests to compare performance based on context, age class, and sex, correct for a multiple comparisons. The study showed that age class and sex did not have a significant effect on performance (Table. 4). Wild monkeys took more trials to complete the task than sanctuary monkeys with a median of 136 trials in the wild compared to 70 trials at the sanctuary (Mann–Whitney $U = 4$, wild: $N = 7$, sanctuary: $N = 7$, $p = 0.041$, Figure. 2). Interestingly, the fastest individuals to complete the task were two adults from the sanctuary. One wild adult male, Fielis (adult male), took 47 trials, while Jokie (adult female) took 30 trials. In the wild, Gaya (adult female) was the fastest individual with 54 trials.

Table. 4: Results from Mann Whitney U tests testing trials to reach learning criterion to pass MTS. N1 and N2 represent the number of individuals for each variable.

	Mann-Whitney U	**N1**	**N2**	**p-value**
Age class	27.5	9 adults	5 juvenile	0.548
Sex	34.5	9 females	5 males	0.125
Context	8	7 wild	7 sanctuary	0.041

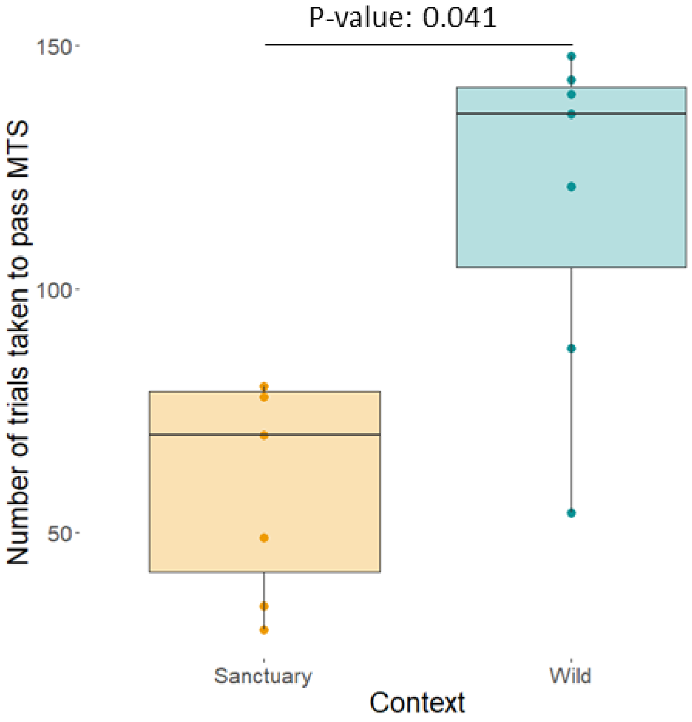


Figure. 2: Represents the number of trials taken by individuals to reach the learning criterion on Match-to-Sample task (MTS). Boxplots show the median in a solid line, first and third quartiles at the upper and lower box edges. Dots represent individuals.

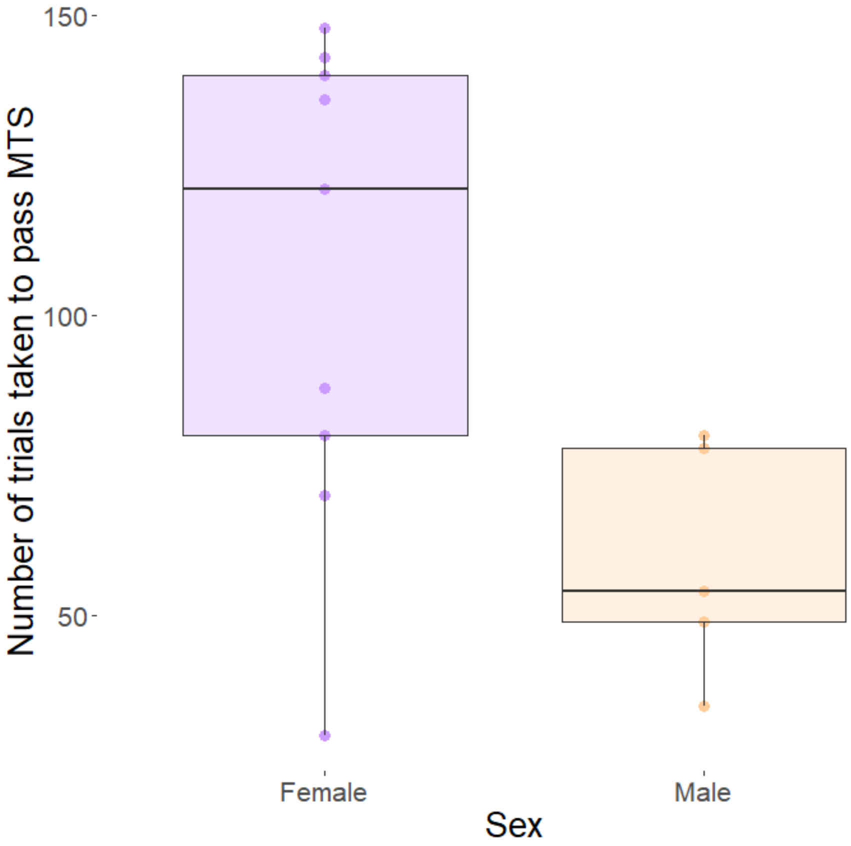


Figure 3: Represents the number of trials taken by individuals to reach the learning criterion on Match-to-Sample task (MTS) between sexes (female vs. male). Boxplots show the median in a solid line, first and third quartiles at the upper and lower box edges. Dots represent individuals.

3.3 Analysis 3: Effect of manual lateralisation on success task

After conducting our analysis, we found that a full model consisting of explanatory variables such as context, age class, sex, side of the correct stimulus, and part of body was a significantly better fit for the data compared to a null model that only considered the individual as a random effect. (X^2 = 17.34, p = 0.008). We did not observe any significant impact of context, age class, or side of the stimulus on performance (Table. 4). Nevertheless, a non-significant trend suggested that sex may have an influence of making the correct choice, as males were less likely to select the correct stimulus than females (est. = -0.21, X^2 = 0.11, p = 0.058, Figure. 4). Additionally, a non-significant trend emerged regarding the probability of making an accurate choice when using the muzzle compared to the left hand (est. = -0.24, X^2 = 0.12, p = 0.050). A post-hoc Tukey test showed that individuals were less likely to select the correct stimulus when using the muzzle in comparison to the right hand (est. = 0.33, X^2 = 0.11, p = 0.008, Figure.

5a). Although individuals were found less likely to succeed when using their muzzle vs. their left hand, this effect did not attain significance when applying a post-hoc Tukey test to account for multiple comparisons. Our findings are available in Table. S4.

Table. 5: Represents the results of GLMM predicting the number of touches taken during experiment 1 in wild and sanctuary population.

Effect	**Estimate**	**Std.Error**	**z-value**	**p-value**
Intercept	0.50	0.14	3.521	0.0004
Context (wild)	0.02	0.11	0.154	0.877
Age class (juvenile)	-0.12	0.11	-1.036	0.300
Sex (male)	-0.21	0.11	-1.895	0.058
Side (right)	0.06	0.09	0.678	0.498
Part Body (Muzzle)	-0.24	0.12	-1.955	**0.050**
Part Body (Right hand)	0.08	0.12	0.712	0.476

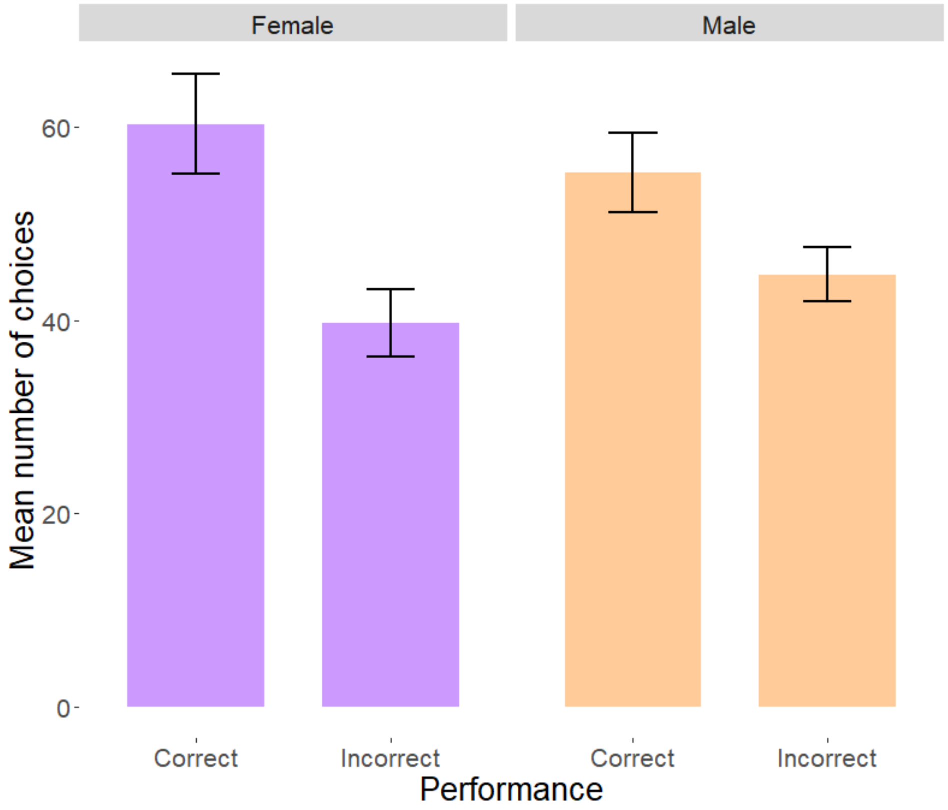


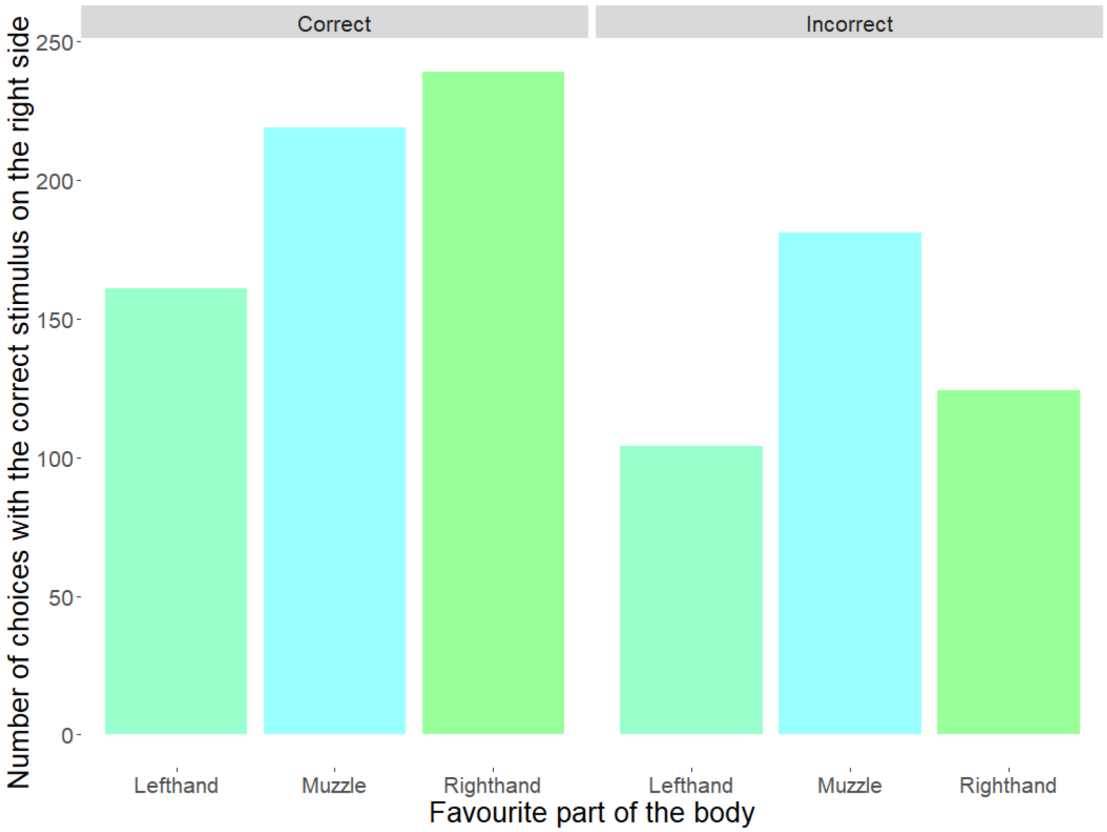
Figure. 4: Represents the mean number of choices correct and incorrect over all experiments, made by females (purple) and males (orange). The bars represent the standard deviation errors.

3.4 Analysis 4: Effect of interaction between favourites part of the body and side of correct touches on success task

In Analysis 3, the full model including the interaction between side of the correct stimulus and favorite part of the bodyprovided a better fit for the data than the null model, which only accounted for the random effect of individual (X^2 = 17.047, p = 0.004). We observed that the probability of correctly selecting the correct choice varied depending on the individuals' preferred body part and the location of the correct stimulus. Specifically, individuals who preferred their muzzle were more likely to choose the correct stimulus when it was on the right side of the screen (est. = -0.58, X^2 = 0.24, p = 0.02, Table. 6). Additionally, from our post-hoc Tukey test we found that individuals who preferred their left hand were more likely to select the left stimulus, while those who preferred their right hand were more likely to select the right stimulus (p = 0.036). Furthermore, we identified a significant interaction between the right side and preferred body part, specifically using muzzle and right hand (p = 0.023). We observed that individuals who preferred their righ hand were less successful when the stimulus was on the left side than the right side of the screen (Supplementary data Table. S4).

Table. 6: Represents the results of GLMM predicting the number of choices taken during MTS in wild and sanctuary population. In this analysis we checked for the influence of the interaction between favourite part of the body and side of the correct stimulus on the number of correct touches.

	Estimate	**Std.Error**	**z-value**	**p-value**
Intercept	0.11	0.14	0.840	0.40
Side (right)	0.31	0.19	1.626	0.01
Favourite Part (muzzle)	0.34	0.18	1.905	0.06
Favourite Part (right hand)	0.07	0.18	0.389	0.69
Interaction Side (right) vs. Favourite Part (muzzle)	-0.58	0.24	-2.388	0.02
Interaction Side (right) vs. Favourite Part (right hand)	0.17	0.25	0.703	0.48


Correct
Incorrect
Number of choices with the correct stimulus on the right side
250
200
150
100
50
0
Lefthand
Muzzle
Righthand
Lefthand
Muzzle
Righthand
Favourite part of the body

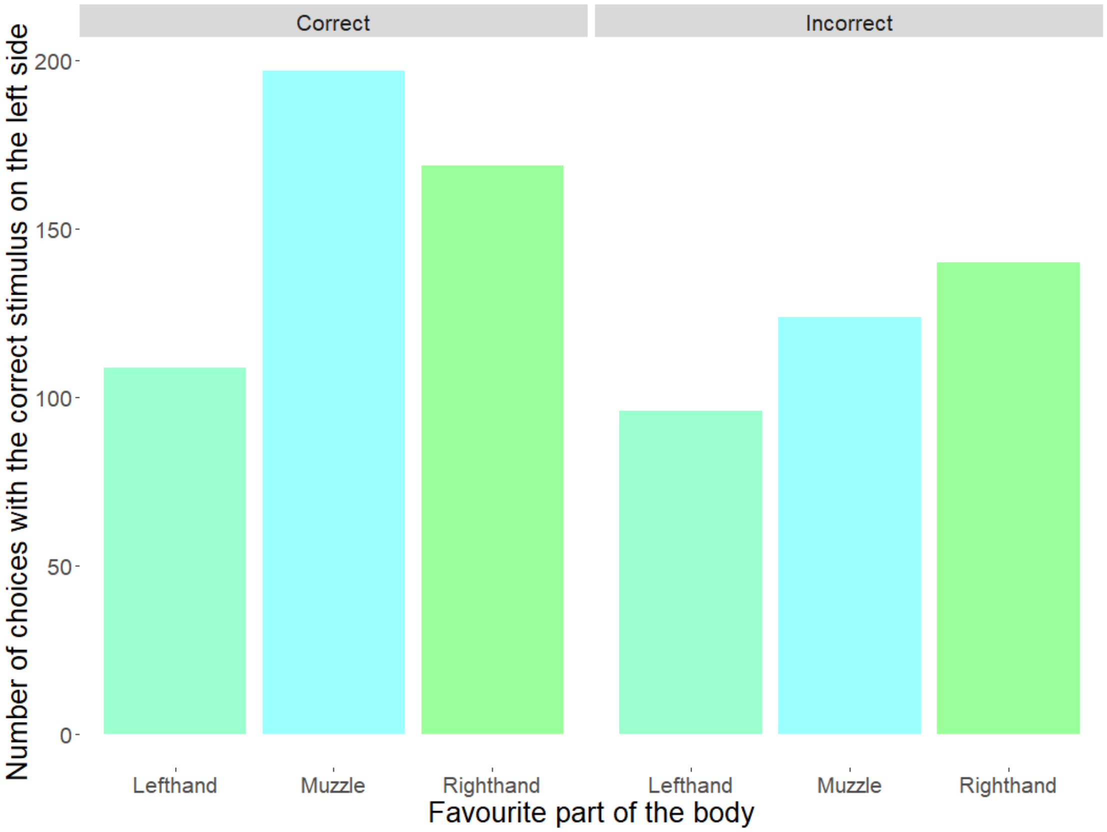

Correct
Incorrect
Number of choices with the correct stimulus on the left side
200
150
100
50
0
Lefthand
Muzzle
Righthand
Lefthand
Muzzle
Righthand
Favourite part of the body

Figure. 5 a, b: Represent the number of correct choices and incorrect choices made by individuals, using three parts of the body (Left hand, Muzzle, Right hand) when the correct stimulus was on the right side (a) and left side (b) of the screen.

3.5 Analysis 5: Reversal learning task

Our study analysed individuals who completed the Reversal Learning Task using 2D stimuli. The participants consisted of seven individuals, including three adult female monkeys from the wild and four individuals from the sanctuary (two adult males and two adult females), as shown in Table. 6. To evaluate performance, we measured the number of trials required to reach the learning criterion for both the Reversal Learning Task (RLT) and the Match-to-sample task (MTS). Our analysis, using a Wilcoxon signed ranks test, revealed a significant difference in the number of trials required to pass both tasks. Specifically, monkeys needed significantly more trials to achieve the criterion on the RLT than on the MTS (V = 1, MTS = RLT: N = 7, p = 0.02, Figure. 6). However, given the small sample size, it was not possible to run any statistical analysis. to compare the number of trials required to pass the RLT according to context (wild vs. sanctuary) and sex (female vs. male).

Table. 6: Represents the list of individuals who passed both MTS and RLT task using 2D stimuli.

Individual	**Group**	**Sex**	**Age class**	**Context**	**Number of trials taken to pass MTS**	**Number of trials taken to pass RLT**
Ginqika	Ankhase	F	Adult	Wild	143	183
Granada	Noha	F	Adult	Wild	148	137
Oortjie	Baie Dankie	F	Adult	Wild	140	246
Boeta	Boeta	M	Adult	Sanctuary	78	151
Fielis	Boeta	M	Adult	Sanctuary	35	118
Jokie	Boeta	F	Adult	Sanctuary	30	181
Poena	Poena	F	Adult	Sanctuary	80	105

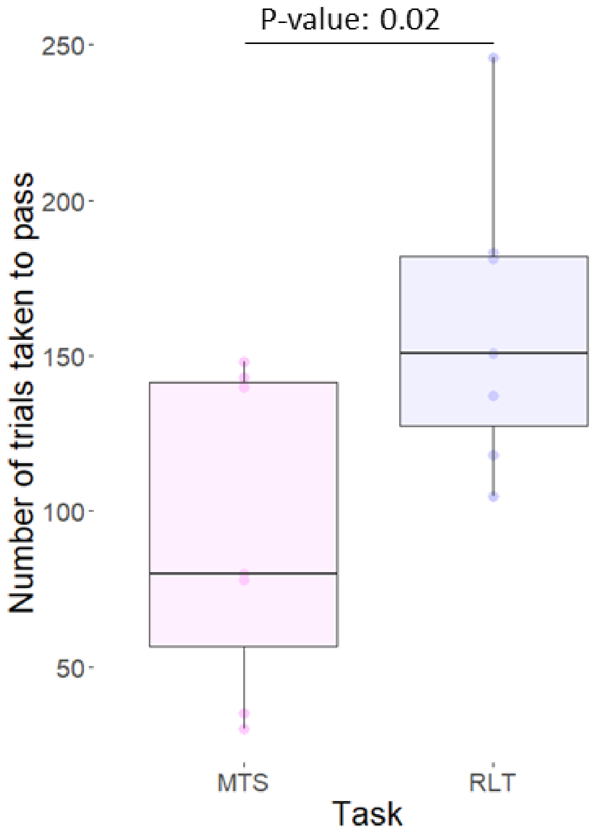


Figure. 6: Represents the number of trials taken by individuals to reach the learning criterion on Match-to-sample task (MTS) and Reversal learning task (RLT). Boxplots show the median in a solid line, first and third quartiles at the upper and lower box edges.

4. Discussion

4.1 Aim and results

Our research contributes to the understanding of the cognitive abilities of wild and sanctuary animals. Specifically, we sought to compare the performance of two groups of vervet monkeys on Match-to-sample and Reversal Learning Tasks. What sets our study apart is the utilization of identical 2D touchscreen tasks and equipment for both populations. Until now, this approach has been absent from previous research, and as a result their cognitive abilities have not been comparatively measured (Harrison et al., 2023).

In our study, we conducted an experiment to assess the performance of sanctuary monkeys when presented with 2D and 3D stimuli tasks. Previous research conducted with chicks (Lee et al., 2012) and young children (Lee & Spelke, 2011) indicated that subjects tend to perform better with 3D stimuli than 2D stimuli. We noted that all sanctuary monkeys which reached criterion on both the 2D and 3D tasks exhibited superior performance and achieved criterion more quickly when presented with 3D stimuli as opposed to 2D stimuli. Although statistical analyses were not feasible due to limited data, upon examining the available data, we observed that four individuals were successful in completing the task using both 2D and 3D stimuli.

4.2 Transfer from 3D to 2D methodology

Both groups of monkeys demonstrated a capacity for learning in their acquisition and mastery of tasks. While only a few individuals successfully completed both the 2D vs. 3D experiments, the learning threshold was attained more rapidly in the experiment utilizing 3D stimuli for both MTS and RLT tasks. Among 17 sanctuary individuals, four were successful in the Match-to-Sample task. Although some individuals passed the criterion using both stimuli, we observed a difference in the number of trials required. Despite the limited number of individuals who met the criterion, these initial findings suggest that vervet monkeys may be capable of associating the correct stimulus in both experimental setups but may require more time to reach the learning threshold on the 2D tasks compared to the 3D tasks. It is possible that the matching process is expedited when presented with tangible stimuli, although monkeys have demonstrated the capacity to use touchscreens and have exhibited proficiency in associating simple stimuli on a screen (Harrison et al., 2023).The 3D stimuli allowed subjects to forage in a more natural way, as they could lift and uncover the rewards, similar to how animals uncover insects under stones. In contrast, the touchscreen required precise hand movements, and the rewards fell to the bottom, providing less direct feedback. Previous research has shown that non-human primates can interpret 3D from 2D stimuli (Vonk et al., 2022). Capuchin monkeys in Truppa et al. (2011) were able to learn a Match-to-Sample task using wooden stimuli but struggled to transfer the knowledge to the same task on the touchscreen. Even if we could not examine more sanctuary individuals due to time constraints and the break between experiments, our findings seems to be in line with previous literature. In the future, training more individuals to use touchscreens would be interesting to increase the sample size, and comparing these abilities within captive and wild groups would be valuable.

4.3 Match-to-sample task

Our study revealed that 14 individuals possess the ability to perform the match-to-sample task using 2D stimuli on a touchscreen. Previous research has shown that captive animals, including non-human primates using touchscreens (Truppa et al., 2011), fish using plates (Aellen et al., 2022) and birds using automated systems (Katz et al., 2008), are capable of learning and memorizing the acquisition rule of cognitive tests using 2D stimuli. Vervet monkeys, known for their discriminative and associative abilities in distinguishing relationships of other group members (Cheney & Seyfarth, 1986) and alarm calls (Strushaker, 1967), were used in a basic associative learning experiment using a touch screen by Harrison et al. (2023). In their study, Harrison et al. (2023) discovered that both sanctuary and wild vervet monkeys needed the same number of trials to reach the learning criterion to pass a basic associative test. However, in our subsequent study in the same populations, we found that sanctuary monkeys reached the learning criterion faster than wild monkeys in a Match-to-Sample task. These results suggest that performance may be influenced by context, but to investigate this further, more data from a larger sample size is required. It is conceivable that the increase in difficulty level, from a single blue square on a white background to a Match-to-Sample task, may have resulted in individuals requiring more time and attention to comprehend the association between stimulus and reward. Despite the difference in group size between the two populations, group members were a distraction when individuals interacted with the touchscreen. In addition, wild monkeys experienced more distractions from the presence of predators and other wild groups compared to sanctuary monkeys, whose distractions were only caused by the presence of items around their enclosure. Prior research has demonstrated that the attendance of zoo visitors does not affect the cognitive task performance of captive primates (Huskisson et al., 2021). Hence, we hypothesized that the activities of keepers would minimally impact our sanctuary population. In the study by Harrison et al. (2023), sanctuary vervet monkeys exhibited higher participation rates compared to their counterparts in the wild. Nonetheless, we noted similar numbers of individuals reaching the learning criterion between the two populations in the experiment. Our project recorded the number of trials for each individual, but we did not measure the duration of each trial. According to Kummer's (1965) free time hypothesis, we anticipated that individuals in sanctuaries would have more free time to devote to tasks than those in the wild. As a result, we predicted that the latter group would perform better.

Although rewards were automatically dispensed, we could not control the level of food motivation amongst individuals. According to the necessity hypothesis, wild individuals are expected to spend more time around the touchscreen as it serves as a potential source of food compared to sanctuary monkeys. Although Harrison et al. (2023) found no evidence of a seasonal influence on participation levels, it is plausible that monkeys may have focused more on succeeding at the task in the winter months due to the lack of food, resulting in a reward of soaked corn as a source of nourishment. The social conflicts arising from the presence of food should not be a factor in the slight decrease in performance of wild monkeys, and it is improbable that their hierarchical position explains it. In future studies, analysing the level of success among ranks would be intriguing. Although previous experiments (Harrison et al., 2023) showed that females spent more time than males, our results did not align with our predictions. The results suggest that males tended to perform better than females in the MTS task, taking fewer trials to pass it. However, females made more choices than males. Furthermore, in various groups of our study population, females have been observed to be dominant (Hemelrijk et al., 2020). Our study found that individuals who were more rewarded, in this case females, demonstrated higher motivation to engage with the touchscreen (Harrison et al., 2023). Interacting with the touchscreen more frequently than males may have increased females' likelihood of making errors. Females required more attempts than males to successfully complete the MTS task.

4.4 Lateralisation influence on performance

Based on these initial findings, we investigated potential factors that could impact the number of correct and incorrect choices made. Our analysis focused on the influence of the body part utilised on an individual's probability of success in the MTS task. Our prediction was based on the lateralisation theory, which suggests that animals use their right or left hand depending on the task's requirements (Vauclair & Fagot, 1987). As the 2D stimuli were presented on either side of the screen, we hypothesized that monkeys would be more likely to choose the correct stimuli if it was on the same side as their dominant hand. Our research revealed that the chances of success in the trials were higher when individuals used their muzzle instead of their left hand. Additionally, the comparison test showed a significant relationship between the side of the body used and the corresponding stimulus. When the stimulus was on the same side as the favoured hand, the monkeys were more likely to choose the correct option. Our findings indicate that individuals made more errors while using their muzzle compared to their right hand. Previous studies on lateralisation demonstrate that a lateralized brain has a direct advantage in learning and problem-solving (Rogers, 2021). During our observation, we noticed only three juvenile individuals who did not exhibit manual lateralisation. None of the three subjects succeeded in utilizing one particular body part over 50% of the time when engaging with the touchscreen. An intriguing discovery we made was that, only one sanctuary individual displayed a preference for using their left hand, while all other subjects opted for their right hand, and no subject showed a consistent preferred use of their muzzle. Conversely, in their natural habitat, a majority of the subjects (eight out of 13) displayed a consistent preference for utilizing their muzzle. It is difficult to ascertain the reason why sanctuary individuals predominantly use their right hand, as we did not measure their brain activity and our sample size was too small to confidently reject any explanations. Our hypothesis was that those who favoured their right hand were more inclined to choose the correct stimuli when presented on the right side of the screen. Further analysis would be beneficial to explore any potential variations in body part preference with varying exposure to the task. It is also possible that individuals who utilise muzzles in the wild may eventually become adept enough to switch to one-handed use.

4.5 Reversal learning task

Once monkeys reached the learning criterion to pass MTS, we tested subjects in a RLT. Wild and sanctuary monkeys took a similar number of trials to reach criterion on the RLT. Only seven out of the 14 individuals reached the learning criterion to pass MTS and RLT. In this last experiment we asked monkeys to choose a previous non rewarded stimulus. The new association led individuals to make more mistakes and very likely may have increased their frustration due to not receiving the desired reward. Previous studies on different taxa showed a trade-off between cognitive flexibility and memory (Tello-Ramos et al., 2019), where individuals, once they learn an association between food-rewarded and stimulus, were slower to adapt when the information changed (Griffin et al., 2013). This difficulty could explain our small sample size, and the reason why individuals who passed MTS needed more trials to pass RLT. From previous experiments in great tits, we know that individuals who persist the most even when they do not succeed in their task are juveniles (Morand-Ferron et al., 2011). In our experiment, we could not test this hypothesis as we did not observe any juvenile who passed the reversal learning experiment. All seven individuals we could test were adults: three wild females, two sanctuary males and two sanctuary females. From our hypothesis, we expected wild individuals to perform better than sanctuary ones. Unfortunately, our sample size was insufficient to test this question. It will be interesting in the future to increase the sample size and study the reversal capacity of juvenile monkeys which previous experiments have indicated to show high levels of cognitive flexibility (Rodriguez et al., 2011).

5. Conclusion

Although a higher number of trials are needed to pass the learning criterion when using 2D stimuli compared to 3D stimuli, our findings demonstrate that touchscreen technology can successfully be employed when working with captive and wild primates. Furthermore, utilising the touchscreen facilitates the comparison of multiple species under the same methodology. Undoubtedly, interacting with wildlife will provide novel insights into animal cognitive abilities within their natural habitats and social groups. Previously, researchers have often extrapolated findings from captive environments to broader species level conclusions. However, with this project, we aspire to establish a new foundation for *in-situ* research through the use of touchscreens in natural conditions.

Acknowledgements

This research received support from both the Swiss National Science Foundation (PP03P3_170624 and PP00P3_198913) and the Branco Weiss Fellowship—Society in Science awarded to Erica van de Waal. The authors extend their gratitude to the van der Walt family for permitting the study to take place at Mawana game reserve and to Sandy Cronk, owner of the rehabilitation centre, for allowing the study to be conducted at W. A. T. C. H.. The authors also express their thanks to Ezemvelo KZN Wildlife for granting permission to perform the research on vervet monkeys in South Africa. We extend our gratitude to M. Henshall for managing the Inkawu Vervet Project and fiield assisting with data collection. We acknowledge the support and aid of the entire IVP team in data collection, with a special mention of T. Henshall, M. German, and S. Glosenger-Thrasher for their valuable assistance in conducting the experiments. We also appreciate the efforts of the students from the EPFL (École Polytechnique Féderale de Lausanne) in supporting the test code.

References

Aellen, M., Siebeck, U. E., & Bshary, R. (2022). Cleaner wrasse Labroides dimidiatus perform above chance in a "matching-to-sample" experiment. *PloS one, 17*(1), e0262351.

Agrillo, C., Petrazzini, M. E. M., & Bisazza, A. (2017). Numerical abilities in fish: a methodological review. *Behavioural processes, 141*, 161-171.

Anderson, C., & Colombo, M. (2022). Matching-to-sample: Comparative overview. *Encyclopedia of Animal Cognition and Behavior*, 4097-4102.

Ashton, B. J., Thornton, A., & Ridley, A. R. (2018). An intraspecific appraisal of the social intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*(1756), 20170288.

Bardo, A., Cornette, R., Borel, A., & Pouydebat, E. (2017). Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology, 164*(4), 821-836.

Bean, A. (2001). 13 Ecology of sex differences in great ape foraging. *Comparative primate socioecology, 22*, 339.

Benson Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta. *Animal behaviour, 85*(2), 349-356.

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (Papio ursinus) and geladas (Theropithecus gelada). *Animal cognition, 12*(1), 63-73.

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal cognition, 13*(5), 701-710.

Blaszczyk, M. B. (2017). Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal behaviour, 123*, 91-100.

Bloch, S., Froc, C., Pontiggia, A., & Yamamoto, K. (2019). Existence of working memory in teleosts: Establishment of the delayed matching-to-sample task in adult zebrafish. *Behavioural brain research, 370*, 111924.

Bono, A. E., Whiten, A., van Schaik, C., Krützen, M., Eichenberger, F., Schnider, A., & van de Waal, E. (2018). Payoff-and sex-biased social learning interact in a wild primate population. *Current Biology, 28*(17), 2800-2805. e2804.

Borgeaud, C., & Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Current Biology, 25*(22), 3011-3016.

Borgeaud, C., Sosa, S., Sueur, C., & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Animal behaviour, 134*, 155-165.

Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. *Animal behaviour, 136*, 1-12.

Boysen, S. T., & Hallberg, K. I. (2000). Primate numerical competence: contributions toward understanding nonhuman cognition. *Cognitive Science, 24*(3), 423-443.

Buchanan, K., & Perera, T. d. (2020). CC-A., & 2012, U.(2020). Guidelines for the treatment of animals in behavioural research and teaching. *Animal behaviour, 159*.

Bussey, T. J., Padain, T. L., Skillings, E. A., Winters, B. D., Morton, A. J., & Saksida, L. M. (2008). The touchscreen cognitive testing method for rodents: how to get the best out of your rat. *Learning & memory, 15*(7), 516-523.

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. *Nature communications, 11*(1), 1-10.

Carere, C., & van Oers, K. (2004). Shy and bold great tits (Parus major): body temperature and breath rate in response to handling stress. *Physiology & behavior, 82*(5), 905-912.

Cauchoix, M., Hermer, E., Chaine, A., & Morand-Ferron, J. (2017). Cognition in the field: comparison of reversal learning performance in captive and wild passerines. *Scientific reports, 7*(1), 1-10.

Cheney, D. L., & Seyfarth, R. M. (1986). The recognition of social alliances by vervet monkeys. *Animal behaviour, 34*(6), 1722-1731.

Clayton, N. (1995). Development of memory and the hippocampus: comparison of food-storing and nonstoring birds on a one-trial associative memory task. *Journal of Neuroscience, 15*(4), 2796-2807.

Cole, E. F., Morand-Ferron, J., Hinks, A. E., & Quinn, J. L. (2012). Cognitive ability influences reproductive life history variation in the wild. *Current Biology, 22*(19), 1808-1812.

Costa, J., Daros, R., Von Keyserlingk, M., & Weary, D. (2014). Complex social housing reduces food neophobia in dairy calves. *Journal of Dairy Science, 97*(12), 7804-7810.

Cox, E., Mancini, C., & Ruge, L. (2020). *Understanding Dogs' Engagement with Interactive Games: Interaction Style, Behaviour and Personality.* Paper presented at the Proceedings of the Seventh International Conference on Animal-Computer Interaction.

Crane, A. L., Brown, G. E., Chivers, D. P., & Ferrari, M. C. (2020). An ecological framework of neophobia: from cells to organisms to populations. *Biological reviews, 95*(1), 218-231.

Crane, A. L., & Ferrari, M. C. (2017). Patterns of predator neophobia: a meta-analytic review. *Proceedings of the Royal Society B: Biological Sciences, 284*(1861), 20170583.

Dongre, P., Canteloup, C., Lanté, G., Cantat, M., & van de Waal, E. (2021). *Role of immigrant males and muzzle contacts in the uptake of a novel food by wild vervet monkeys.* (PhD)

Douglas, L. A., Varlinskaya, E. I., & Spear, L. P. (2003). Novel-object place conditioning in adolescent and adult male and female rats: effects of social isolation. *Physiology & behavior, 80*(2-3), 317-325.

Fabre-Thorpe, M., Fagot, J., Lorincz, E., Levesque, F., & Vauclair, J. (1993). Laterality in cats: paw preference and performance in a visuomotor activity. *Cortex, 29*(1), 15-24.

Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. *Psychological bulletin, 109*(1), 76.

Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior research methods, 41*(2), 396-404.

Fagot, J., Thompson, R. K., & Parron, C. (2010). How to read a picture: Lessons from nonhuman primates. *Proceedings of the National Academy of Sciences, 107*(2), 519-520.

Fairbanks, L. A. (1993). Risk-taking by juvenile vervet monkeys. *Behaviour, 124*(1-2), 57-72.

Ferrari, M. C., & Chivers, D. P. (2008). Cultural learning of predator recognition in mixed-species assemblages of frogs: the effect of tutor-to-observer ratio. *Animal behaviour, 75*(6), 1921-1925.

Forss, Motes-Rodrigo, A., Dongre, P., Mohr, T., & van de Waal, E. (2021). Captivity and habituation to humans raise curiosity in vervet monkeys. *Animal cognition*, 1-12.

Fugazza, C., Moesta, A., Pogány, Á., & Miklósi, Á. (2018). Social learning from conspecifics and humans in dog puppies. *Scientific reports, 8*(1), 1-10.

Galef, B. G., McQUOID, L. M., & Whiskin, E. E. (1990). Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. *Animal Learning & Behavior, 18*(2), 199-205.

Galef Jr, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal behaviour, 61*(1), 3-15.

Gareta García, M., Lemieux, D., & Bshary, R. (2021). Factors affecting tolerance persistence after grooming interactions in wild female vervet monkeys, Chlorocebus pygerythrus.

Greenberg. (1990). Ecological plasticity, neophobia, and resource use in birds. *Studies in Avian Biology*.

Greenberg. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. *Animal innovation*.

Greenberg, & Mettke-Hofmann. (2001). Ecological aspects of neophobia and neophilia in birds. *Current ornithology*, 119-178.

Griffin, A. S., Guez, D., Lermite, F., & Patience, M. (2013). Tracking changing environments: innovators are fast, but not flexible learners. *PloS one, 8*(12), e84907.

Grilly, D. M. (1975). Sex differences in delayed matching-to-sample performance of chimpanzees. *Psychological Reports, 37*(1), 203-207.

Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates opportunities for chimpanzee tool use. *Behavioral Ecology, 30*(4), 1136-1144.

Gunhold, T., Whiten, A., & Bugnyar, T. (2014). Video demonstrations seed alternative problem-solving techniques in wild common marmosets. *Biology letters, 10*(9), 20140439.

Gutierrez, R. (2023). Studying behavior under constrained movement. *Elife, 12*, e91145.

Haakonsson, J. E., & Semple, S. (2009). Lateralisation of trunk movements in captive Asian elephants (Elephas maximus). *Laterality, 14*(4), 413-422.

Healy, S. D., & Hurly, T. A. (2013). What hummingbirds can tell us about cognition in the wild. *Comparative Cognition & Behavior Reviews*.

Hemelrijk, C. K., Wubs, M., Gort, G., Botting, J., & van de Waal, E. (2020). Dynamics of intersexual dominance and adult sex-ratio in wild vervet monkeys. *Frontiers in psychology, 11*, 839.

Hopper, L. M. (2017). Cognitive research in zoos. *Current Opinion in Behavioral Sciences, 16*, 100-110.

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal cognition, 17*(4), 835-847.

Hunter, W. S. (1948). The delayed reaction in animals and children, 1914.

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science, 354*(6308), 110-114.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 308*(1135), 203-214.

Isparta, S., Demirbas, Y. S., Bars, Z., Kul, B. C., Güntürkün, O., Ocklenburg, S., & Pereira, G. D. G. (2020). The relationship between problem-solving ability and laterality in cats. *Behavioural brain research, 391*, 112691.

Lamon, N., Neumann, C., & Zuberbühler, K. (2018). Development of object manipulation in wild chimpanzees. *Animal behaviour, 135*, 121-130.

Lee, P. C., & Antonio, C. d. A. (2015). Necessity, unpredictability and opportunity: An exploration of ecological and social drivers of behavioral innovation. In *Animal creativity and innovation* (pp. 317-333): Elsevier.

Lee, S. A., & Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychonomic bulletin & review, 18*, 192-198.

Lee, S. A., Spelke, E. S., & Vallortigara, G. (2012). Chicks, like children, spontaneously reorient by three-dimensional environmental geometry, not by image matching. *Biology letters, 8*(4), 492-494.

Lefeuvre, M., Gouat, P., Mulot, B., Cornette, R., & Pouydebat, E. (2022). Analogous laterality in trunk movements in captive African elephants: a pilot study. *Laterality, 27*(1), 101-126.

Li, M. F.,Arseneau-Robar, T. J. M., Smeltzer, E. A., & Teichroeb, J. A. (2021). Be early or be tolerated: vervet monkey, Chlorocebus pygerythrus, foraging strategies in a dispersed resource. *Animal behaviour, 176*, 1-15.

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

Lind, J., Enquist, M., & Ghirlanda, S. (2015). Animal memory: A review of delayed matching-to-sample data. *Behavioural processes, 117*, 52-58.

MacDonald, S. E., & Ritvo, S. (2016). Comparative cognition outside the laboratory. *Comparative Cognition & Behavior Reviews, 11*.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., Brooks, M. M. (2017). Package 'glmmtmb'. *R Package Version 0.2. 0*.

Marchetti, K., & Price, T. (1989). Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological reviews, 64*(1), 51-70.

Markowitz, H. (1982). *Behavioral enrichment in the zoo*: van Nostrand Reinhold.

Martin, C. F., Muramatsu, A., & Matsuzawa, T. (2022). Apex and ApeTouch: Development of a Portable Touchscreen System and Software for Primates at Zoos. *Animals, 12*(13), 1660.

Martina, C., Cowlishaw, G., & Carter, A. J. (2021). Individual differences in task participation in wild chacma baboons. *Animal behaviour, 172*, 73-91.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature, 315*(6014), 57-59. Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. *Chimpanzee cultures*, 351-370.

McBride, S. D., Perentos, N., & Morton, A. J. (2016). A mobile, high-throughput semi-automated system for testing cognition in large non-primate animal models of Huntington disease. *Journal of neuroscience methods, 265*, 25-33.

Miller, R., Bugnyar, T., Pölzl, K., & Schwab, C. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology, 69*(7), 1209-1220.

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: associative learning in wild great tits. *PloS one, 10*(8), e0133821.

Morand-Ferron, J., Wu, G.-M., & Giraldeau, L.-A. (2011). Persistent individual differences in tactic use in a producer–scrounger game are group dependent. *Animal behaviour, 82*(4), 811-816.

Mueller-Paul, J., Wilkinson, A., Aust, U., Steurer, M., Hall, G., & Huber, L. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (Chelonoidis carbonaria). *Behavioural processes, 106*, 187-192.

O'Hara, M., Mioduszewska, B., von Bayern, A., Auersperg, A., Bugnyar, T., Wilkinson, A., Gajdon, G. K. (2017). The temporal dependence of exploration on neotic style in birds. *Scientific reports, 7*(1), 1-9.

Paquette, D., & Prescott, J. (1988). Use of novel objects to enhance environments of captive chimpanzees. *Zoo Biology, 7*(1), 15-23.

Plueckhahn, T. C. (2022). *The relationship between motor lateralisation, temperament and problem-solving in the domestic dog (Canis familiaris): Investigating common measures and methods.*

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

Rachel, H., Tecla, M., & Erica, V. d. W. (2023). Lab cognition going wild: Implementing a new portable touchscreen system in vervet monkeys. *Animal Ecology*.

Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of natural stimuli by domestic dogs. *Animal cognition, 11*, 339-347.

Rodriguez, J. S., Zürcher, N. R., Bartlett, T. Q., Nathanielsz, P. W., & Nijland, M. J. (2011). CANTAB delayed matching to sample task performance in juvenile baboons. *Journal of neuroscience methods, 196*(2), 258-263.

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1519), 943-954.

Rogers, L. J. (2018). Manual bias, behavior, and cognition in common marmosets and other primates. *Progress in Brain Research, 238*, 91-113.

Rössler, T., Mioduszewska, B., O'Hara, M., Huber, L., Prawiradilaga, D. M., & Auersperg, A. M. (2020). Using an Innovation Arena to compare wild-caught and laboratory Goffin's cockatoos. *Scientific reports, 10*(1), 1-12.

Ruff, H. A., Saltarelli, L. M., Capozzoli, M., & Dubiner, K. (1992). The differentiation of activity in infants' exploration of objects. *Developmental psychology, 28*(5), 851.

Schaffer, A., Caicoya, A. L., Colell, M., Holland, R., von Fersen, L., Widdig, A., & Amici, F. (2021). Neophobia in 10 ungulate species—a comparative approach. *Behavioral Ecology and Sociobiology, 75*(7), 102.

Schmitt, V. (2018). Implementing new portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. *bioRxiv*, 316042.

Schuett, W., Tregenza, T., & Dall, S. R. (2010). Sexual selection and animal personality. *Biological reviews, 85*(2), 217-246.

Schuppli, C., Forss, S., Meulman, E., Atmoko, S. U., van Noordwijk, M., & van Schaik, C. (2017). The effects of sociability on exploratory tendency and innovation repertoires in wild Sumatran and Bornean orangutans. *Scientific reports, 7*(1), 1-12.

Schuppli, C., Forss, S. I., Meulman, E. J., Zweifel, N., Lee, K. C., Rukmana, E., van Schaik, C. P. (2016). Development of foraging skills in two orangutan populations: needing to learn or needing to grow? *Frontiers in zoology, 13*, 1-17.

Schuppli, C., van Cauwenberghe, A., Setia, T. M., & Haun, D. (2021). The ontogeny of exploratory object manipulation behaviour in wild orangutans. *Evolutionary Human Sciences, 3*.

Seed, A., & Byrne, R. (2010). Animal tool-use. *Current Biology, 20*(23), R1032-R1039.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science, 210*(4471), 801-803.

Sherratt, T. N., & Morand-Ferron, J. (2018). The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal behaviour, 138*, 59-67.

Shettleworth, S. J. (2000). Modularity and the evolution of cognition. *The evolution of cognition, ed. CM Heyes & L. Huber*, 43-60.

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal behaviour, 61*(2), 277-286.

Skinner, B. F. (1988). Preface to the behavior of organisms. *Journal of the Experimental Analysis of Behavior, 50*(2), 355.

Stephan, C., Wilkinson, A., & Huber, L. (2012). Have we met before? Pigeons recognise familiar human faces. *Avian Biology Research, 5*(2), 75-80.

Stöwe, M., Bugnyar, T., Heinrich, B., & Kotrschal, K. (2006). Effects of group size on approach to novel objects in ravens (Corvus corax). *Ethology, 112*(11), 1079-1088.

Strushaker, T. (1967). Auditory communication among vervet monkeys. *Cercopithecus aethiops*.

Szabo, B., Valencia-Aguilar, A., Damas-Moreira, I., & Ringler, E. (2022). Wild cognition–linking form and function of cognitive abilities within a natural context. *Current Opinion in Behavioral Sciences, 44*, 101115.

Takola, E., Krause, E. T., Müller, C., & Schielzeth, H. (2021). Novelty at second glance: a critical appraisal of the novel object paradigm based on meta-analysis. *Animal behaviour, 180*, 123-142.

Team, R. C. (2013). R: A language and environment for statistical computing.

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

Therneau, T. M., & Therneau, M. T. M. (2015). Package ‘coxme’. *R package version, 2*(5).

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 978-987.

Thornton, A., & Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2773-2783.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science, 313*(5784), 227-229.

Tomasello, M., & Call, J. (1994). Social cognition of monkeys and apes. *American Journal of Physical Anthropology, 37*(S19), 273-305.

Truppa, V., Piano Mortari, E., Garofoli, D., Privitera, S., & Visalberghi, E. (2011). Same/different concept learning by capuchin monkeys in matching-to-sample tasks. *PloS one, 6*(8), e23809.

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate’s foraging decisions. *Science, 340*(6131), 483-485.

van de Waal, E., & Bshary, R. (2010). Contact with human facilities appears to enhance technical skills in wild vervet monkeys (Chlorocebus aethiops). *Folia Primatologica, 81*(5), 282-291.

van de Waal, E., Claidière, N., & Whiten, A. (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. *Animal cognition, 18*(3), 617-627.

van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matrilines in wild vervet monkeys. *PloS one, 7*(4), e35694.

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society of London B: Biological Sciences, 277*(1691), 2105-2111.

an Horik, J. O., Langley, E. J., Whiteside, M. A., & Madden, J. R. (2017). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural processes, 134*, 22-30.

Vauclair, J., & Fagot, J. (1987). Spontaneous hand usage and handedness in a troop of baboons. *Cortex, 23*(2), 265-274.

Visalberghi, E., Janson, C., & Agostini, I. (2003). Response toward novel foods and novel objects in wild Cebus apella. *International Journal of Primatology, 24*(3), 653-675.

Wallace, J., Steinert, P. A., Scobie, S. R., & Spear, N. E. (1980). Stimulus modality and short-term memory in rats. *Animal Learning & Behavior, 8*(1), 10-16.

Washburn, D. A., & Rumbaugh, D. M. (1992). Testing primates with joystick-based automated apparatus: Lessons from the Language Research Center’s Computerized Test System. *Behavior Research Methods, Instruments, & Computers, 24*(2), 157-164.

Webb, S. J. N., Hau, J., & Schapiro, S. J. (2019). Relationships between captive chimpanzee (Pan troglodytes) welfare and voluntary participation in behavioural studies. *Applied animal behaviour science, 214*, 102-109.

Wolff, M., Benhassine, N., Costet, P., Segu, L., & Buhot, M.-C. (2004). Interaction between the nature of the information and the cognitive requirement of the task in problem solving in mice. *Cognitive brain research, 21*(3), 289-300.

Wood-Gush, D., & Vestergaard, K. (1991). The seeking of novelty and its relation to play. *Animal behaviour, 42*(4), 599-606.

Yin, J., Yu, G., Zhang, J., & Li, J. (2023). Behavioral laterality is correlated with problem-solving performance in a songbird. *Animal cognition, 26*(3), 837-848.

Zajonc, R. B. (1965). Social Facilitation: A solution is suggested for an old unresolved social psychological problem. *Science, 149*(3681), 269-274.

Zentall, T. R., & Smith, A. P. (2016). Delayed matching-to-sample: A tool to assess memory and other cognitive processes in pigeons. *Behavioural processes, 123*, 26-42.

3. General discussion

The objective of this thesis is to compare the cognitive abilities of wild and sanctuary vervet monkeys via the use of touchscreen technology. To ensure that the experiment is not influenced by external factors in wild animals, I have taken steps to test all variables. Thus, I assessed a) the initial interaction of sanctuary and wild vervet monkeys with a touchscreen b) the impact of environmental factors on experiment participation, and c) the performance differences between sanctuary and wild monkeys when presented with 2D and 3D stimuli in both a Match-to-Sample and Reversal Learning Task, and the influence of the part of the body used on their performance. I presented the outcomes of diverse issues, deliberated on conceivable explanations for them, and assessed the benefits and drawbacks of incorporating a touchscreen in a natural setting. Moreover, I proposed some developments and recommendations for potential further investigations.

3.1 Summary findings

According to the free time hypothesis, captive animals should possess additional free time and energy to innovate and explore in contrast to wild individuals who encounter steady daily constraints (Kummer & Goodall, 1985). Therefore, it is possible that the free time hypothesis may account for our findings, which revealed that sanctuary monkeys presented shorter latencies in approaching the touchscreen, spent more time interacting with it than their wild counterparts (as observed in Chapter 1), and exhibited higher levels of participation than wild monkeys (as discussed in Chapter 2).

The study presented in Chapter 1 provides evidence that sanctuary monkeys exhibited differing behaviours upon their initial exposure to touchscreens than wild monkeys. These results corroborate earlier findings from novelty experiments which demonstrated that captive primates were more inclined to engage with novel objects and foods compared to their wild counterparts (Benson Amram et al., 2013; Forss et al., 2021).

Being hand raised by humans until the age of three months may have influenced the behaviour and confidence of animals in the sanctuary towards humans and the physical environment. Even though sanctuary monkeys were inexperienced with touchscreens, they were acquainted with televisions and cell phones used by staff at the centre. Both televisions and cell phones exhibited 2D images that resembled the stimuli presented on the touchscreen (Sharp, 2017). Furthermore, it is plausible that both the wild and sanctuary monkeys regarded the touchscreen as a secure and intriguing item since it was delivered by a familiar individual (Forss et al., 2021).

Both populations had participated in previous experiments involving boxes (Botting et al., 2018; Canteloup et al., 2020; Gareta García et al., 2021; van de Waal et al., 2015a). Ochieng-Odero (1994) suggested that domestication involves both habituation and conditioning to environmental stimuli present frequently. This may explain our results with the enculturation hypothesis influencing monkeys behaviours towards objects brought in by researchers. Consequently, our findings show that both populations (wild and sanctuary monkeys) exhibited a similar preference for interacting with the touchscreen using their hands rather than their muzzles.

Building on the findings of our study, which revealed significant differences in touchscreen interaction time and participation between wild and captive monkeys, Chapter 3 presents a comparison of wild and sanctuary primates in MTS and RLT tasks involving 2D and 3D stimuli. The results indicate that sanctuary monkeys were more proficient at matching 3D stimuli compared to 2D. Nonetheless, both sanctuary group displayed some abilities in completing the MTS task using both types of stimuli. We observed a noteworthy discrepancy in the ability to pass MTS tasks than RLT. Regrettably, only four out of the 30 subjects were successful when presented with both tasks. Due to the small sample size, statistical analysis could not be performed. Additionally, our analysis investigated the impact of context on MTS task performance using 2D stimuli displayed via touchscreen. Notably, sanctuary monkeys exhibited superior performance in achieving the Match-to-Sample task learning criteria compared to wild monkeys. The results need cautious analysis due to the limited sample size. Therefore, I recommend conducting more research to verify the robustness of the outcomes with a larger sample. Additionally, I aspire that my study sparks the use of touchscreen technology in natural environments and encourages replicating confining experiments with conspecifics.

Unfortunately, the composition of the sanctuary groups was such that a comparative analysis between age and sex class categories was not possible. Therefore, I could only analyse differences in age and sex class among wild vervet monkey groups. In all three chapters, wild adult females were the most active individuals in age and sex class, as they exhibited more exploratory behaviours, spent more time interacting with touchscreens and consequently participated in more tasks compared to males. Vervet hierarchy is based on codominance between males and females (Young et al., 2019). However, in IVP, it has been shown that females are dominant over males and many groups have a female as the most dominant individual in the group (Hemelrijk et al., 2020). Our results show that females were more persistent and monopolised the touchscreen than males. In many primates species, such as in vervets, females have an important role related to foraging, looking after their offspring and territory defence. The dominant role of female may be one of the factor that explain the high level of participation with the touchscreen

3.2 The impact of captivity on animal cognitive abilities and the role of enrichment

Captive animals housed in controlled environments may experience a deficit in cognitive stimulation, involving foraging, defending the territory, and facing predators which may account for their mental abilities being less varied than those of their wild counterparts (Meehan et al., 2007, see review Boesch, 2021). Without adaptive problem-solving or complex decision-making, captive animals may not fully develop certain cognitive skills that are crucial for survival in their natural habitat (Tomasello, 1997). Furthermore, the enclosed environments can result in the formation of behavioural stereotypies, which are repetitive actions without apparent purpose that may indicate dissatisfaction or boredom (Mason, 1985; Pomerantz et al., 2013). For example, in a captive study in rhesus macaque, researchers have observed two main stereotypic behaviours such as hair-pulling and pacing (Lutz et al., 2003). These behavioural patterns have considerable implications concerning animal welfare and conservation and, therefore, the cognitive performance of captive individuals may not be representative to that of the wild-living (see review Boesch, 2021).

Enrichment activities, similar to real-life problem-solving situations, significantly boost exploration, improve cognitive abilities, and contribute to better psychological health (Young, 2013). An important component of the integration of appropriate challenge into the environments of captive animals is providing opportunities for animals to apply cognitive skills in the process of solving problems (Clark, 2017; Meehan et al., 2007). These animals must navigate a complex terrain where every decision shapes their ability to obtain food, protect their territory, find a mate, and evade predators (Szabo et al., 2022). The development of mental faculties in wild animals is a continuous interplay between genetic predispositions and environmental pressures (Amodio et al., 2018; Hopkins et al., 2015). Such a dynamic interaction shapes cognition uniquely compared to that of captive animals.

Foraging behaviour provides an example of the different levels of analysis that can be applied to assessing the effects of enrichment techniques. For example, in food acquisition skills in the wild animals deal with a wide array of challenges associated with procuring large, mobile, patchy, or temporally available food items (McLean, 2001). Which evolved adaptability and cognitive skills to solve problems. While it is the case that the captive context will greatly restrict opportunities to incorporate these complex behaviours into foraging opportunities, the facilitation of the cognitive mechanisms which underlie their performance could be addressed through the integration of appropriate challenge into foraging enrichment strategies, with opportunities to engage in activities that invigorate their senses, encourage exploration, and challenge their cognitive skills may lead to a more fulfilling and healthier captivity experience overall.

Studying cognition in natural settings provides a valuable and distinct standpoint for understanding animal behaviour. It uncovers the adaptive cognitive processes that evolve in response to the daily exigencies of survival. In contrast to captive animals, their wild counterparts encounter a broad range of environmental challenges. offering objective insights into the adaptive nature of cognitive processes, providing a comprehensive understanding of how cognition evolves to meet specific ecological challenges.

3.3 Advantage and disadvantages to study captive and wild animals

Cognitive experiments carried out on captive animals are a fundamental aspect of scientific research that aid in comprehending the anatomy, behaviour, cognition, and ecology of species (Rees, 2015). Studies conducted in neuroscience and biomedical laboratories, for instance, entail direct manipulation of the animal, such as employing electrodes (O'Keefe & Dostrovsky, 1971; Wilson & McNaughton, 1993) and administering chemicals (Franco, 2013). While these studies may lead to valuable knowledge, they raise ethical and animal welfare concerns (Jayne & See, 2019). Laboratory animals are frequently isolated from their peers and subjected to testing in solitary environments, leading to elevated stress levels. For instance, captive dogs and piglets that live in isolated enclosures display dissimilar behaviour such as attempts to escape, fear-related behaviours and reduced playfulness in comparison to social animals (Herskin & Jensen, 2000; Hubrecht et al., 1992). In zoos where animals have the freedom to move around without direct human contact, they reside in regulated surroundings which vary significantly from their native habitats where wild animals live in social groups, vast territories and ever-changing biomes. Although attempts have been made to replicate an ecologically and socially close environment to the wild, the limited space and resources of these facilities make it impracticable to provide optimum conditions for the animals' stay but guarantee animal welfare that surpasses the quality of care offered in laboratory settings (Learmonth, 2019). In both natural habitats and captive environments, animal behaviour is influenced by social group dynamics (Aplin et al., 2014; Croney & Newberry, 2007; Estevez et al., 2007). The limited number of individuals in captivity can lead to issues such as isolation and depression (Olsson & Westlund, 2007; Woolverton et al., 1989). In contrast, individuals within a social group have the chance to acquire skills essential for their survival, such as foraging or social and hierarchical abilities, by learning from other group members. Moreover, the existence of barriers restricts the movement of specific individuals, especially those that would naturally disperse, thus causing instability within the hierarchy of the group. The confinement of either excessively large or small groups in a confined area leads to issues of competition and aggression (Pacheco, 2018). The provision of food and water in animal enclosures promotes animal wellbeing. However, constant access to these resources can create competition among animals and lead to behavioural changes that limit foraging activity during the day (Jaman & Huffman, 2008; Schwitzer & Kaumanns, 2003). In captivity, the absence of predators is another limiting factor, particularly when considering the cognitive aspect of animals. Animals inhabiting natural environments have frequently adapted to interact and respond to them, such as by fleeing or alerting others to the presence of potential dangers (see review Evans et al., 2019; Gill & Bierema, 2013; Seyfarth et al., 1980). In nature, animals remain vigilant at all times, while the absence of danger in captivity results in a decreased level of alertness due to the perception of a secure environment. While the lack of natural predators can increase animals' odds of survival, it may also lead to boredom and frustration in captivity. As a result, some zoos and centres have begun implementing enrichment programs that promote physiological and cognitive stimulation for the animals (McPhee & Carlstead, 2010; Morgan & Tromborg, 2007). In addition, in some research places an automatic system has been developed where animals are recognised by chips or collars and are free to interact with the set-up when and how they want (Fagot & Bonté, 2010; Hopper, 2017), thus decreasing the need to isolate the tested individuals and thus the stress level. Research on captive animals provides the opportunity to conduct research in order to increase our knowledge also in the field of conservation, which can answer questions of reproduction, reintroduction, and population management. But while the controlled aspect and proximity to animals in captivity may answer some behavioural questions, direct field studies allow us to observe animals in a natural context where they can express their behaviour, such as their ability to adapt to seasonal and climatic changes (Papageorgiou et al., 2021; Ullmann et al., 2023), and their relationships (Borgeaud et al., 2017; Brask et al., 2021; Pacheco, 2018). Although animals can be free to express themselves in the wild, for researchers the study of animals in a natural context has limitations: Animals not being restricted by enclosures are free to move around and are therefore elusive and difficult to observe. In addition, the dense vegetation during the rainy seasons creates a hidden and safe place. Like the animals, the dense vegetation also influences researchers. Tall grasses, such as plants or flooding rivers, are natural obstacles to collecting data. In natural contexts, it is difficult to control unpredictable factors such as weather conditions or predation. In addition, the distance of animal homerange limits the maintenance and supply of certain devices that require, for example, the use of power. Not least, the field study can pose risks for researchers, especially if they study dangerous animals or are within their territory. In order to facilitate the search for wild animals, some researchers have developed technologies such as radio collars and GPS location (Aguzzi et al., 2011; Bonter & Bridge, 2011), which require animals to be captured and tagged. As well as causing stress and behavioural change, close proximity with researchers can be a danger to both parties in the transmission of diseases. Through scratches, bites or contact with bodily fluids, wild animals can transmit pathogens such as viruses, bacteria and parasites that are known as zoonotic diseases, as they can be transmitted to humans (Fong & Fong, 2017; Kruse et al., 2004). But while animals can transmit diseases to humans, researchers can also be sources of danger for the animals themselves. Humans can transmit, in rare cases, diseases to animals through direct handling. This can cause epidemics or fatal diseases in wild animal populations (Messenger et al., 2014).

3.4 Advantage and disadvantage to study monkeys at IVP and W. A. T. C. H.

One of the key benefits of the research conducted in this thesis is the pioneering approach of examining wild animals through the application of touchscreen. Although the use of this technology is widespread for captive animals, it has never previously been tested in wild contexts. While the monkeys studied in this thesis have been tracked since 2010, they have experienced no direct interaction with researchers. The primates are not kept in captivity, but instead inhabit their natural environment where they are exposed to natural predators. Their freedom of movement between groups makes them ideal subjects for study (Dongre, 2022). In the winter months, the savannah bush becomes barren, causing the monkeys to face challenges in finding sufficient food and water. Conversely, in summer, the bush flourishes with new leaves, fruits and flowers. Despite this, our thesis did not identify any evidence of seasonality impacting primate participation (see Supplemental information Chapter 2).

Despite my best efforts to ensure the safety of the monkeys, certain external factors, such as predators and neighbouring groups, remained beyond my control. If the monkeys encountered an alarm call, whether produced by themselves or other individuals, I had to cease the experiment. The presence of predators often caused the monkeys to become terrified, hindering their movement for extended periods of time while perched atop trees. Alternatively, following the alarm call, the monkeys would quickly move away from their sleeping area and seek shelter in low-lying bushes (Seyfarth et al., 1980). In both scenarios, the motivation of the monkeys decreased, necessitating the discontinuation of the experiment. Between October and March, the birthing season for both adult and three-year-old female monkeys, I observed new mothers exhibiting two distinct behaviours. Some moved away from the touchscreen, likely seeking protection for their infants, while others displayed increased motivation to approach and obtain food, presumably as a result of physiological needs. In an unenclosed environment like the wilderness, I was unable to regulate the dispersal season, which allowed males to disperse to nearby clusters. One hindrance encountered during my thesis was that a few males dispersed while the experiments were ongoing, thus failing to finish the assigned experimental tasks. If the males had dispersed within the monitored groups, the experiments could have proceeded. This is illustrated by the dispersal of two males from Ankhase to Baie Dankie. Having recently moved to the new group, the two males had limited access to the touchscreen. Additionally, three males from Noha separated into different groups and were unable to be located. To ensure the continuity of the experiment, it is advisable to utilise tracking collars to determine their whereabouts. A former colleague of mine trained male primates to open peanuts, an unfamiliar food source, before they were introduced to new groups (Dongre, 2022). The study observed the innovative and transmitted information within the dispersal group. The findings revealed that the trained males were the primary source of the information, with the rest of the group following their lead in opening and consuming the peanuts.

It would be fascinating to replicate her research using various tasks on touchscreens. One of the benefits of studying primates at the IVP research site is the ability to observe male dispersal. Although these primates are highly habituated, their behaviour does not appear to be affected enough to deviate from their natural behaviour. Studying wild monkeys may be more appropriate for observing their behaviour without human interference. However, modifications to the methodology are necessary for studying these creatures. Please refer to the section on ethics for further details.

Unfortunately, a major issue encountered in operating a rehabilitation centre is the composition of each enclosure. The composition of groups at W. A. T. C. H. was based on the number of orphans rescued in previous years, leading to an unnatural age-sex ratio in certain groups. This resulted in the presence of individuals ranging from three months to five years old within the enclosures. The maximum number of adults available during the experiment was three individuals in Boeta's group, three females and four males in Poena's group, one female and one male in Liffie's group, and two females in Cowen's group. The limited number of adults precluded a statistical analysis of the influence of age on performance and participation. Boeta's group was the only group to include older adults with 16 and 17 years-old individuals. Although I treated all individuals over five years old as adults during the analyses, I was unable to account for the duration of time they spent confined in the enclosure. It is plausible that individuals who were confined for an extended period could have been more severely impacted than those who were confined for a shorter time. In the future, it would be appropriate to conduct tests on a larger sample and control for the potential impact of time spent in enclosures on animals' cognitive abilities. All primates studied at the centre were rescued a few days or months after birth and despite early human contact, after three months they lived without it. Their inclusion as study models for predicting enculturation hypotheses makes vervet monkeys an excellent addition to human research (Forss et al., 2021; van de Waal et al., 2015b). Moreover, monkeys live in groups with atypical compositions and are often kept confined within enclosures where they do not need to forage or protect themselves from predators. Consequently, the stress levels in W. A. T. C. H. are likely to be lower than those observed in laboratory-monitored monkeys. However, when they are in enclosures, monkeys are unable to move and disperse as freely as they would in the wild. Furthermore, they are unable to escape or avoid conflicts with higher-ranking individuals.

3.5 Advantage and disadvantage to study monkeys using touchscreen

In recent decades, touchscreens have emerged as an innovative methodology for studying neurology in laboratory animals and cognitive abilities, such as memory and recognition, in free-range animals. This project aims to expand this methodology to wild animals. The studies of Seitz (2021) and Fagot (2010) have contributed to the development of this field. For my thesis, I conducted three main tasks: classical associative learning, a match-to-sample task, and Reversal Learning Task. In order to enable the study of wild monkeys, an automated apparatus was essential, eliminating the need for human proximity. Nevertheless, humans were still required to identify monkeys that approached the touchscreen, to ensure correct task presentation on the screen. To develop a portable field system, we had to design an autonomous code within the Matlab and psychtoolbox software (Matlab, 2012). The infrared around the screen allowed the code to receive the monkey's touch coordinates (Schmitt, 2018). It then activated a portable battery which rotated a food dispenser, releasing soaked corn, if the touch was within the stimulus. The code was utilised to remotely control the identification of the monkey operating the touchscreen from an iPad via a Wi-Fi connection. Once the field assistants ensured that everything was working, they could independently conduct the experiment, which was particularly helpful when I was absent. The technological system also caused some minor inconveniences during the experiment. The key factor enabling the use of the touchscreen in the outdoors was the availability of a portable ECU battery system. This battery was fully charged the previous night before the experiment. The presence of such a battery system addressed the issue of insufficient electricity supply in the field. However, electricity shortages frequently occurred during the summer at the IVP field house. Owing to prolonged electric power outages and thunderstorms, several days were experienced without electricity, rendering a complete charging of the battery unfeasible.

Another issue encountered during the experiments related to the food dispenser and its tube. Blockages in the dispenser could discourage the monkeys from interacting with the touchscreen. Therefore, it was crucial to select corn of uniform size that could be dispensed easily. Despite careful selection, at times one or more corn kernels became wedged under the dispenser tray. Once the primates felt at ease, they displayed significant curiosity towards the apparatus. After determining the origin of the food, they displaced the tube of the food dispenser, obstructing the pathway for corn to drop into the reward hole. It may be advantageous in the future to stabilise the tube with a material that cannot be easily taken or destroyed by the monkeys. Lastly, a hindrance we faced with the use of the touchscreen interface was the infrared connection. In order to transmit touch coordinates to the computer, it was essential that the infrared remained free from dirt, sand, or any other vegetation present on the monkey's hand. This ensured that the system remained automatic and free from any potential biases that may arise from human observation. On many occasions, it became necessary to pause the experiment, clean the infrared, and start again. The use of Wi-Fi was also crucial, as it allowed for distance to be maintained between the apparatus and the monkeys, enabling even the shyest of individuals to approach. Unfortunately, the Wi-Fi I employed had a 10-meter range limit when placed in an open space. Therefore, prior to commencing the experiment, it was necessary to clear the area in front of the screen of tall vegetation, branches, or brush, as their presence could disrupt the Wi-Fi signal. Although measures were taken to regulate the distance, level, and cleanliness of the vegetation near the apparatus, some factors such as the weather continued to pose challenges. On foggy and cloudy days, the Wi-Fi connection was disrupted and slower than on normal days. At W. A. T. C. H. the presence of houses and other sources of Wi-Fi at also contributed to the disruption of the connection between the iPad and the touchscreen. To ensure accuracy, I always turned off the Wi-Fi in the adjacent house before conducting the experiment. The transportation of the touchscreen from the house to the sleeping sites and enclosures posed the greatest challenge in my thesis. The equipment was initially designed for use with chimpanzees in a zoo (Schmitt, 2018). I modified it for studying wild vervet monkeys at the beginning of this project (see Supplemental information Chapter 2), but even after the alterations, it weighed around 15 kilograms. Transporting the metal box with trays was not feasible as the unsteady and rugged terrain of the bush would not allow it. Each morning, I, with assistance from other field assistants, carried the equipment on our backs as we crossed rivers, hills and dense vegetation. This approach facilitated accessing remote sleeping sites. However, it limited the experimentation frequency and locations.

3.6 Identity of the individual present over the period of the experiment

Numerous scientific studies have been conducted on various animal species in laboratory and zoo settings (see review McEwen et al., 2022). While the introduction of advanced technology, such as touchscreens, has led to the exploration of cognitive abilities like memory retention, image discrimination, and facial recognition in animals, there is a lack of research on their initial response towards touchscreens (Egelkamp & Ross, 2019). This research can only be conducted on animals residing in free-range habitats such as zoos, sanctuaries, or the wild. In these settings, the animals have the freedom to decide whether and how to approach the touchscreen (Bergman & Kitchen, 2009), unlike in laboratory conditions, where the animals are isolated and confined in front of the screen (Gutierrez, 2023). In novel experiments, animals should first become familiar with the new apparatus, food, or object by interacting and exploring it. Normally, in order to investigate how animals approach novel objects, researchers motivate individuals by placing some familiar food nearby (Forss et al., 2021). It has been observed that the individual who first approaches and interacts with the apparatus usually monopolizes it and achieves the highest level of performance (Thornton & Lukas, 2012). Long-term interaction with the device resulted in enhanced problem-solving abilities, surpassing those who did not engage regularly (Morand-Ferron et al., 2011). Although a constant level of participation was observed within the monkey groups throughout the experiment, certain individuals chose to depart after a few months or stopped participating altogether, owing to reasons such as sexual maturation, which leads to dispersal of males, and the birth of new offspring for females. In the following section, I will elaborate on the individuals who continued participating from the beginning of the experiment until the last experiment.

Here is a summary of the individuals' interactions with the touchscreen throughout the experiment, including those who began interacting later (see Table supplements). Among five wild groups, a total of 37 individuals approached the touchscreen during the initial exposure (Chapter 1). However, only three of these individuals were able to reach the final learning criterion for the Reversal Learning Task (Chapter 3). Moreover, due to the absence of individuals at the field site due to Covid-19, it was not feasible to continue with Lemon Tree's group. Consequently, Lemon Tree's data could not be collected for Chapter 2 and Chapter 3. Regrettably, due to juveniles' dominance and adults' inadequate motivation to engage with the touchscreen, we were unable to observe any individuals in Kubu's group who completed the training tasks. Therefore, for Chapter 3, we utilised data from only three groups. Ankhase, Baie Dankie and Noha. During the experiment timeframe, three male individuals belonging to Noha's groups were not traceable and are presumed to have dispersed to vervet groups beyond our study population. The three remaining individuals from Noha group, Granada, Guatemala, Griselle in Noha were all from the same dominant matriline. During our experiments in Baie Dankie, we observed a juvenile male who participated in all tasks and successfully completed the Match-to-Sample task (Chapter 2). However, his access to the touchscreen was limited due to the dominance of his two older sisters, Oerwound and Oortjies. While the female siblings were motivated to approach and interact with the touchscreen, their mother chose to remain aloof. In Chapter 1, she approached the touchscreen but did not interact during the experiment in Chapter 2, most likely due to a lack of confidence towards humans. The absence of the dominant mother permitted her daughters to monopolise the touchscreen. Both sisters successfully completed the Reversal Learning Task, but only one met the learning criterion in Chapter 3. Unfortunately, significant alterations were made to the females' hierarchy in Ankhase group during the experiment period owing to the loss of the alpha female. For an extended period, the identification of the dominant female was elusive as two adult daughters, Gubha and Ginqinka, competed for the role. Both females were involved in the experiment, but at separate intervals (Chapter 2). The elder sibling, Gubha, initially interacted with the touchscreen on the first day (Chapter 1), but subsequently ceased doing so in the ensuing weeks and was replaced by her younger sister, Ginqika, who took over as the alpha individual. From that point on, Ginqika monopolized the touchscreen throughout the entire period, ultimately achieving the learning criterion for the Reversal Learning Task (Chapter 3). Gilane took control of one of the two testing tasks, the Match-to-Sample task, when his mother allowed him to approach the touchscreen in Ankhase. During the first experiment, two brothers from a low rank matriline, Nakhu and Ngenakubo, were also present. They approached the touchscreen together, supporting each other. Ngenakubo, the elder brother, did not finish the Reversal Learning Task as he joined Baie Dankie's group before completing the final task. On the other hand, his younger brother, Nakhu, accomplished the match-to-sample experiment, but he also followed his brother to Baie Dankie's group after a few months.

For Chapter 1, we analysed three of the groups, all of which were exposed to the touchscreen. To ensure accessibility for all individuals, the touchscreen was attached to the enclosure fence using hooks.

During the first experiment, we observed 21 individuals from the three sanctuary groups who approached the apparatus. However, only seven of them managed to reach the Match-to-Sample task, and out of those, only four were able to reach the Reversal Learning Task. Liffie's group was among the first groups to interact with the touchscreen, and there were nine individuals in the group. Although the group actively participated in the experiment, they were released into the wild in 2019. Unfortunately, it was not possible to proceed with the experiment as the monkeys were not equipped with any tracking devices. My thesis entails assessing the abilities of monkeys in the wild and those at the sanctuary. In the future, it would be intriguing to track the progress of released animals and continue with the experimental setup to investigate whether the transition from a controlled and safe environment to a natural and hazardous one could affect their cognitive abilities. The second group I examined at the sanctuary was Boeta's group. All three individuals successfully completed both learning tasks, Match-to-Sample and Reversal Learning Task (Chapter 3). Comprising two elderly males and one elderly female whose participation remained constant, the group was the smallest we tested. The third group tested was Poena's group. Throughout the experiment, three individuals were consistently present (Chapter 2). One fully grown female used to exclusively monopolize the touchscreen, deterring any other individuals from approaching it. Although attempts were made to distract her with some corn on the opposite side of the enclosure, she only permitted Gizmo, the dominant juvenile male, to interact with the apparatus. While the initial young male was granted the opportunity to engage with the touchscreen, Fanjan had to compel the participation of the other juvenile. The subordinate male displayed greater strength throughout the experiment, finally ascending the hierarchy. Due to insufficient daily observation, it was not possible to establish the hierarchy. Our assumptions were therefore based on the dominant female's tolerance around the touchscreen. It was noted that only the adult female achieved the learning criterion for the Reversal Learning Task (Chapter 3). Cowen's data was removed from the analysis in Chapter 1, due to a different experimental setup. Despite being unable to utilise Cowen's data for the first exposition, a high participation was observed throughout the experiment (Chapter 2). Cowen's group solely featured juvenile monkeys. In 2020, only two females gave birth to their first offspring and reached adulthood. Following Rainbow's delivery, as the dominant female, she became more cautious when approaching the touchscreen. However, she used to chase away any members attempting to get near it, excluding the dominant male, who was responsible for monopolising it.

3.7 Improvement and future directions

In order to enhance the transportation of the touchscreen device, it would be advantageous to reduce its size in the future. This would permit the transfer of multiple touchscreens simultaneously, consequently reducing the impact of monopolisation on participation. Such high participation levels could also result in an increased collection of data. To address the issue of monopolization, we could train individuals to recognize visual patterns on the screen that signal their turn to interact with the touchscreen. This strategy would help ensure a balanced sample size in terms of age and sex group (Borgeaud & Bshary, 2015). Additionally, reducing the size and weight of the equipment would allow for the presence of only one or two field assistants. When working with wild animals, it is crucial to consider their level of habituation (Forss et al., 2021). Certain individuals exhibit indifference towards human presence, while others tend to maintain distance. In order to encourage shy and fearful individuals to approach the box, it may be beneficial to have fewer humans present around the touchscreen, which could boost their confidence and motivation. Previous experiments have employed advanced technological methods such as automatic facial recognition (Schofield et al., 2019) or radio frequency identification (Fagot & Paleressompoulle, 2009; Morand-Ferron et al., 2015) to assess free-ranging animals. It would be appropriate for future studies to incorporate one of these approaches into the touchscreen system, allowing automatic identification of individuals and presentation of relevant tasks. With the implementation of protective structures, the touchscreen could remain in the field for longer periods of time. In my thesis, I observed certain social patterns that impacted the participation and performance of individuals. Therefore, it would prove beneficial to utilise proximity loggers in future studies to examine the influence of social networks surrounding the touchscreen. It must be noted that these methods could lead to stress on the animals, necessitating their capture and sedation. Therefore, I suggest this approach solely for animals that require this procedure for standard reasons, such as routine husbandry procedures. For unhabituated species, it may be more beneficial to establish a system using remote control or camera traps for individual recognition. This method would be an effective solution for reducing manipulative stress on wild animals and refining techniques to minimize our impact on wildlife.

The use of fully automatic systems offers researchers several ethical benefits concerning animal welfare. Firstly, animals can interact with the equipment while remaining in their natural habitats instead of being captured and taken into captivity. Animals need to be motivated to interact with the apparatus, which can often be achieved by offering familiar treats that are low in calories to avoid disrupting their routine or behaviour. One of the primary difficulties in examining animals using rewards is the potential association they may form between humans and food. This link could result in addiction, which in extreme cases could pose a risk to both the researcher and the animal (Fedigan, 2010). If animals associate humans with food, it could lead to hazards not only for researchers or field assistants but also for nearby residents, especially if the species inhabits areas close to dwellings. The second benefit of employing an automatic system in wild animals is to reduce the likelihood of animals associating food with human presence. The third benefit is to lower the possibility of transmitting or acquiring zoonotic infections, which are diseases that can be transmitted between animals and humans (Day et al., 2012). For instance, during the coronavirus pandemic, we ensured the safety of animals by disinfecting the touchscreen after every experiment. Working with remote or automatic devices would reduce the possibility of transmitting any infection from humans to wild animals. This approach would not only ensure the safety of animals but also minimize the risk of researchers being bitten or scratched.

In the future, the incorporation of these advancements, alongside our touchscreen system, could remove all limitations in studying mammalian species in their natural habitats. Animals could be studied without the inherent risks associated with disease transmission, resulting in more accurate representation of natural animal behaviours.

References

Aguzzi, J., Sbragaglia, V., Sarriá, D., García, J. A., Costa, C., del Río, J., Sardà, F. (2011). A new laboratory radio frequency identification (RFID) system for behavioural tracking of marine organisms. Sensors, 11(10), 9532-9548.

Amodio, P., Jelbert, S. A., & Clayton, N. S. (2018). The interplay between psychological predispositions and skill learning in the evolution of tool use. Current Opinion in Behavioral Sciences, 20, 130-137.

Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. Proceedings of the Royal Society B: Biological Sciences, 281(1789), 20141016.

Benson Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta. Animal behaviour, 85(2), 349-356.

Boesch, C. (2021). Identifying animal complex cognition requires natural complexity. Iscience, 24(3).

Bonter, D. N., & Bridge, E. S. (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. Journal of Field Ornithology, 82(1), 1-10.

Borgeaud, C., Sosa, S., Sueur, C., & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. Animal behaviour, 134, 155-165.

Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. Animal behaviour, 136, 1-12.

Brask, J. B., Ellis, S., & Croft, D. P. (2021). Animal social networks: an introduction for complex systems scientists. Journal of Complex Networks, 9(2), cnab001.

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. Nature communications, 11(1), 459.

Clark, F. E. (2017). Cognitive enrichment and welfare: Current approaches and future directions. Anim. Behav. Cogn, 4(1), 52-71.

Croney, C. C., & Newberry, R. C. (2007). Group size and cognitive processes. Applied animal behaviour science, 103(3-4), 215-228.

Dongre, P. (2022). Integrating dispersal and social learning in vervet monkeys (Chlorocebus pygerythrus). éditeur non identifié.

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. Zoo Biology, 38(2), 220-235.

Estevez, I., Andersen, I.-L., & Nævdal, E. (2007). Group size, density and social dynamics in farm animals. Applied animal behaviour science, 103(3-4), 185-204.

Evans, D. A., Stempel, A. V., Vale, R., & Branco, T. (2019). Cognitive control of escape behaviour. Trends in cognitive sciences, 23(4), 334-348.

Fagot, J., & Bonté, E. (2010). Automated testing of cognitive performance in monkeys: Use of a battery of computerized test systems by a troop of semi-free-ranging baboons (Papio papio). Behavior research methods, 42, 507-516.

Fong, I., & Fong, I. (2017). Animals and mechanisms of disease transmission. Emerging Zoonoses: A Worldwide Perspective, 15-38.

Forss, Motes-Rodrigo, A., Dongre, P., Mohr, T., & van de Waal, E. (2021). Captivity and habituation to humans raise curiosity in vervet monkeys. Animal cognition, 1-12.

Franco, N. H. (2013). Animal experiments in biomedical research: a historical perspective. Animals, 3(1), 238-273.

Gareta García, M., Lemieux, D., & Bshary, R. (2021). Factors affecting tolerance persistence after grooming interactions in wild female vervet monkeys, Chlorocebus pygerythrus.

Gill, S. A., & Bierema, A. M. K. (2013). On the meaning of alarm calls: a review of functional reference in avian alarm calling. Ethology, 119(6), 449-461.

Gutierrez, R. (2023). Studying behavior under constrained movement. Elife, 12, e91145.

Hemelrijk, C. K., Wubs, M., Gort, G., Botting, J., & Van de Waal, E. (2020). Dynamics of intersexual dominance and adult sex-ratio in wild vervet monkeys. *Frontiers in psychology, 11*, 839.

Herskin, M., & Jensen, K. (2000). Effects of different degrees of social isolation on the behaviour of weaned piglets kept for experimental purposes. Animal Welfare, 9(3), 237-249.

Hopkins, W. D., Reamer, L., Mareno, M. C., & Schapiro, S. J. (2015). Genetic basis in motor skill and hand preference for tool use in chimpanzees (Pan troglodytes). Proceedings of the Royal Society B: Biological Sciences, 282(1800), 20141223.

Hopper, L. M. (2017). Cognitive research in zoos. Current Opinion in Behavioral Sciences, 16, 100-110.

Hubrecht, R. C., Serpell, J. A., & Poole, T. B. (1992). Correlates of pen size and housing conditions on the behaviour of kennelled dogs. Applied animal behaviour science, 34(4), 365-383.

Jaman, M. F., & Huffman, M. A. (2008). Enclosure environment affects the activity budgets of captive Japanese macaques (Macaca fuscata). American Journal of Primatology: Official Journal of the American Society of Primatologists, 70(12), 1133-1144.

Jayne, K., & See, A. (2019). Behavioral research on captive animals: scientific and ethical concerns. In Animal Experimentation: Working Towards a Paradigm Change (pp. 517-547): Brill.

Kruse, H., Kirkemo, A.-M., & Handeland, K. (2004). Wildlife as source of zoonotic infections. Emerging Infectious Diseases, 10(12), 2067.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 308(1135), 203-214.

Learmonth, M. J. (2019). Dilemmas for natural living concepts of zoo animal welfare. Animals, 9(6), 318.

Lutz, C., Well, A., & Novak, M. (2003). Stereotypic and self-injurious behavior in rhesus macaques: a survey and retrospective analysis of environment and early experience. American Journal of Primatology: Official Journal of the American Society of Primatologists, 60(1), 1-15.

Mason, W. (1985). Experiential influences on the development of expressive behaviors in rhesus monkeys. The development of expressive behavior, 117-152.

Matlab, S. (2012). Matlab. The MathWorks, Natick, MA.

McEwen, E. S., Warren, E., Tenpas, S., Jones, B., Durdevic, K., Rapport Munro, E., & Call, J. (2022). Primate cognition in zoos: Reviewing the impact of zoo-based research over 15 years. American Journal of Primatology, 84(10), e23369.

McPhee, M. E., & Carlstead, K. (2010). The importance of maintaining natural behaviors in captive mammals. Wild mammals in captivity: Principles and techniques for zoo management, 2, 303-313.

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: can problem solving opportunities enhance animal welfare? Applied animal behaviour science, 102(3-4), 246-261.

Messenger, A. M., Barnes, A. N., & Gray, G. C. (2014). Reverse zoonotic disease transmission (zooanthroponosis): a systematic review of seldom-documented human biological threats to animals. PloS one, 9(2), e89055.

Morand-Ferron, J., Wu, G.-M., & Giraldeau, L.-A. (2011). Persistent individual differences in tactic use in a producer–scrounger game are group dependent. Animal behaviour, 82(4), 811-816.

Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. Applied animal behaviour science, 102(3-4), 262-302.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: preliminary evidence from unit activity in the freely-moving rat. Brain research.

Ochieng'-Odero, J. (1994). Does adaptation occur in insect rearing systems, or is it a case of selection, acclimatization and domestication? International Journal of Tropical Insect Science, 15, 1-7.

Olsson, I. A. S., & Westlund, K. (2007). More than numbers matter: The effect of social factors on behaviour and welfare of laboratory rodents and non-human primates. Applied animal behaviour science, 103(3-4), 229-254.

Pacheco, M. X. P. (2018). Social network structure and personality in captive meerkat, Suricata suricatta, populations: assessment, comparison between wild and captive meerkat populations and captive management implications: University of Exeter (United Kingdom).

Papageorgiou, D., Rozen-Rechels, D., Nyaguthii, B., & Farine, D. R. (2021). Seasonality impacts collective movements in a wild group-living bird. Movement Ecology, 9(1), 1-12.

Pomerantz, O., Meiri, S., & Terkel, J. (2013). Socio-ecological factors correlate with levels of stereotypic behavior in zoo-housed primates. Behavioural processes, 98, 85-91.

Rees, P. A. (2015). Studying captive animals: A workbook of methods in behaviour, welfare and ecology: John Wiley & Sons.

Schmitt, V. (2018). Implementing new portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. bioRxiv, 316042.

Schwitzer, C., & Kaumanns, W. (2003). Foraging patterns of free-ranging and captive primates-implications for captive feeding regimes. Zoo animal nutrition, 2, 247-265.

Seitz, B. M., McCune, K., MacPherson, M., Bergeron, L., Blaisdell, A. P., & Logan, C. J. (2021). Using touchscreen equipped operant chambers to study animal cognition. Benefits, limitations, and advice. PloS one, 16(2), e0246446.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science, 210(4471), 801-803.

Sharp, L. A. (2017). The moral lives of laboratory monkeys: television and the ethics of care. Culture, Medicine, and Psychiatry, 41, 224-244.

Szabo, B., Valencia-Aguilar, A., Damas-Moreira, I., & Ringler, E. (2022). Wild cognition–linking form and function of cognitive abilities within a natural context. Current Opinion in Behavioral Sciences, 44, 101115.

Thornton, A., & Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1603), 2773-2783.

Tomasello, M., & Call, J. (1997). Primate cognition: Oxford University Press, USA.

Ullmann, W., Fischer, C., Kramer-Schadt, S., Pirhofer Walzl, K., Eccard, J. A., Wevers, J. P., . . . Glemnitz, M. (2023). The secret life of wild animals revealed by accelerometer data: How landscape diversity and seasonality influence the behavioural types of European hares. Landscape Ecology, 1-15.

van de Waal, E., Claidière, N., & Whiten, A. (2015a). Wild vervet monkeys copy alternative methods for opening an artificial fruit. Animal cognition, 18(3), 617-627.

van de Waal, E., Claidière, N., & Whiten, A. (2015b). Wild vervet monkeys copy alternative methods for opening an artificial fruit. Animal cognition, 18, 617-627.

Wilson, M. A., & McNaughton, B. L. (1993). Dynamics of the hippocampal ensemble code for space. Science, 261(5124), 1055-1058.

Woolverton, W., Ator, N. A., Beardsley, P., & Carroll, M. E. (1989). Effects of environmental conditions on the psychological well-being of primates: A review of the literature. Life sciences, 44(14), 901-917.

Young, R. J. (2013). Environmental enrichment for captive animals: John Wiley & Sons.

Young, C., McFarland, R., Ganswindt, A., Young, M. M., Barrett, L., & Henzi, S. P. (2019). Male residency and dispersal triggers in a seasonal breeder with influential females. *Animal behaviour, 154*, 29-37.

4.Supplemental information

4.1 Supplemental Information Chapter 1

Table. S1: Total presentation time's experiment per group.

Context	**Group**	**Total presentation time (min)**
Wild	Ankhase	28.20
	Baie Dankie	40.98
	Kubu	70.45
	Lemontree	53.33
	Noha	37.04
Sanctuary	Boeta	28.25
	Liffie	34.31
	Poena	32.68

Table. S2: Latency to approach the touchscreen for each group. Latency to approach the touchscreen varied between individuals, so minimum and maximum latency are shown.

Context	**Group**	**Minimum Latency (min)**	**Maximum Latency (min)**
Wild	Ankhase	1.47	14.38
	Baie Dankie	0.80	37.54
	Kubu	1.60	35.30
	Lemontree	0.43	28.66
	Noha	0.15	31.59
Sanctuary	Boeta	0.18	6.17
	Liffie	0.06	1.70
	Poena	0.15	3.02

Table. S3: Latency to approach the touchscreen for each individual between age and sex classes. Minimum and maximum latency to approach the touchscreen are shown.

Context	**Group**	**Age and Sex classes**	**Minimum Latency (min)**	**Maximum Latency (min)**
Wild	Ankhase	Juvenile Female	6.73	6.73
		Juvenile Male	1.47	3.86
		Adult Female	1.74	14.38
		Adult Male	NA	NA
	Baie Dankie	Juvenile Female	0.80	11.93
		Juvenile Male	3.38	7.85
		Adult Female	0.85	27.33
		Adult Male	1.62	37.54
	Kubu	Juvenile Female	NA	NA
		Juvenile Male	10.55	10.55
		Adult Female	6.90	35.30
		Adult Male	1.60	1.60
	Lemontree	Juvenile Female	0.86	28.66
		Juvenile Male	0.70	16.31
		Adult Female	0.43	15.65
		Adult Male	3.04	8.40
	Noha	Juvenile Female	0.91	5.77
		Juvenile Male	13.07	13.07
		Adult Female	0.15	0.15
		Adult Male	2.14	31.59

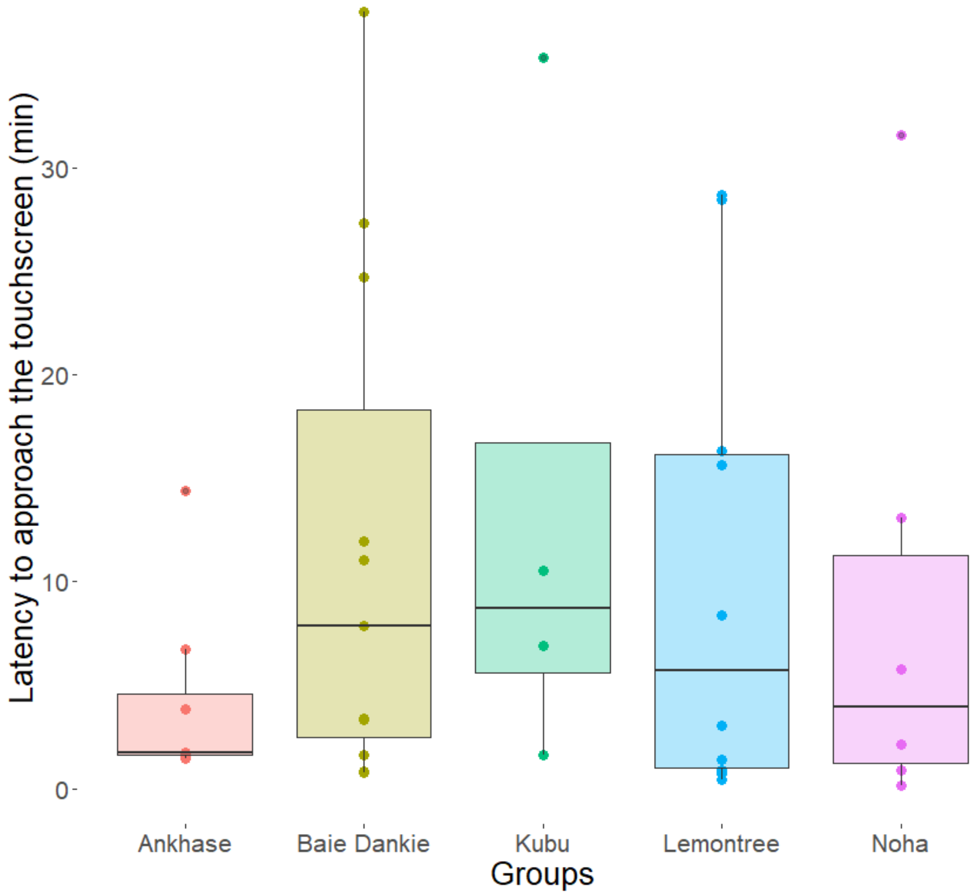


Figure. S1: Boxplot showing the distribution of the latency by five wild groups, with solid horizontal lines showing the median latency, upper and lower limits of the box showing the first and third quartiles and points representing the latency observed in each individual, coloured by Group.

Table. S4: Details time interacting with the touchscreen in each group. Time individuals interacted with the touchscreen varied between individuals. Minimum and maximum latency are shown.

Group	Context	Minimum Time interacting (min)	Maximum Time interacting (min)
Wild	Ankhase	0.29	9.12
	Baie Dankie	0.13	9.93
	Kubu	0.25	31.75
	Lemontree	0.25	29.94
	Noha	1.39	26.81
Sanctuary	Boeta	2.75	15.64
	Liffie	4.35	22.97
	Poena	2.02	27.42

Table. S5: Results of post-hoc Tukey test predicting the time interacting with the touchscreen for each group in wild population only.

	Estimate	Std. Error	z	p-value
Baie Dankie - Ankhase == 0	0.05941	0.46420	0.128	0.9999
Kubu - Ankhase == 0	1.54876	0.62455	2.480	0.0929
Lemontree - Ankhase == 0	0.89618	0.47008	1.906	0.3088
Noha - Ankhase == 0	0.78913	0.53809	1.467	0.5790
Kubu - Baie Dankie == 0	1.48935	0.58218	2.558	0.0763
Lemontree - Baie Dankie == 0	0.83677	0.42985	1.947	0.2878
Noha - Baie Dankie == 0	0.72972	0.49907	1.462	0.5820
Lemontree - Kubu == 0	-0.65258	0.59261	-1.101	0.8026
Noha - Kubu == 0	-0.75963	0.63952	-1.188	0.7544
Noha - Lemontree == 0	-0.10705	0.50841	-0.211	0.9996

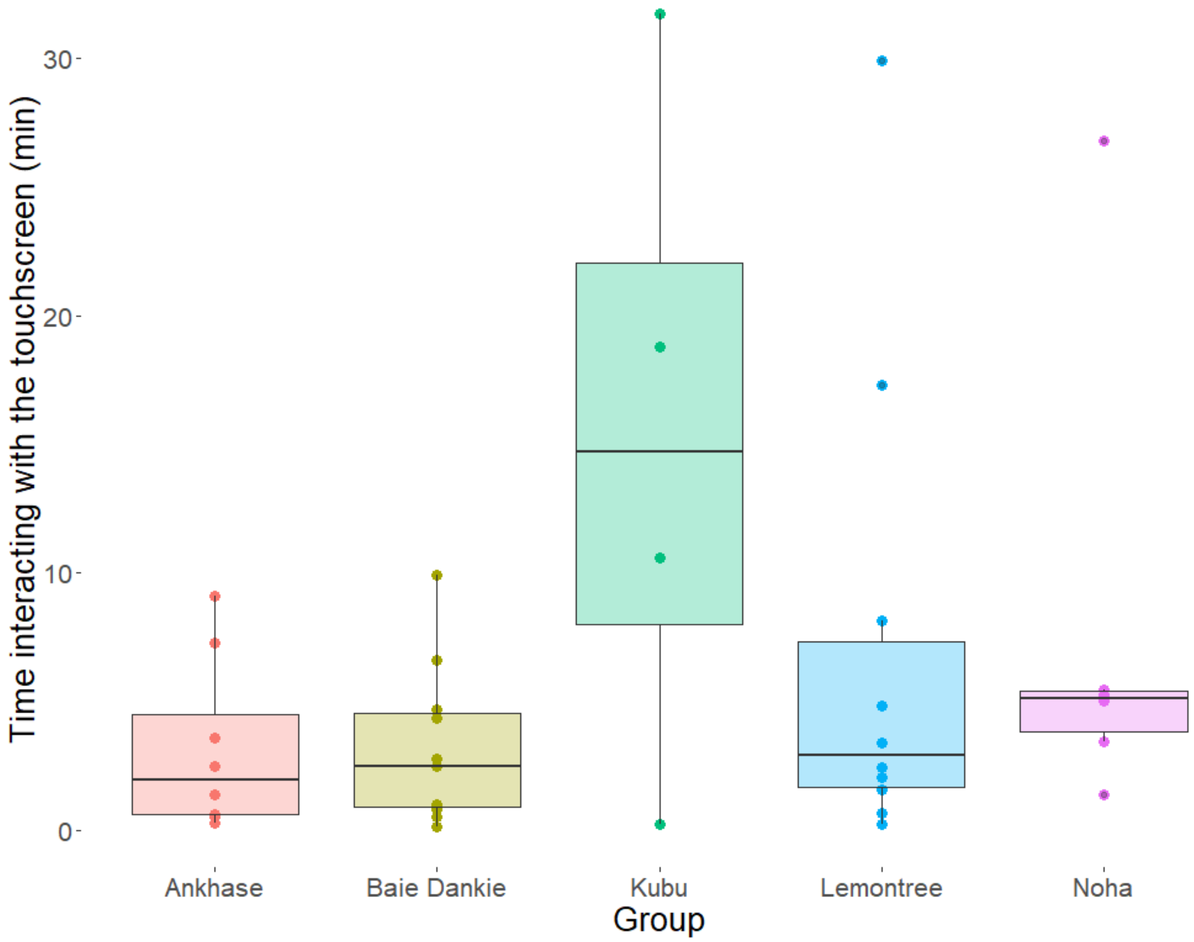


Figure. S2: Boxplot showing the distribution of the time interacting with the touchscreen by five wild groups, with solid horizontal lines showing the median latency, upper and lower limits of the box showing the first and third quartiles and points representing the time each individual spent interacting with the touchscreen, coloured by Group.

Table. S6: Details time interacting for each individual between age and sex classes. Minimum and maximum time are shown.

Context	Group	Age and Sex classes	Minimum Time interacting (min)	Maximum Time interacting (min)
Wild	Ankhase	Juvenile Female	2.47	2.47
		Juvenile Male	0.29	3.59
		Adult Female	7.28	9.12
		Adult Male	NA	NA

Baie Dankie	Juvenile Female	0.82	4.68
	Juvenile Male	0.13	4.37
	Adult Female	0.53	9.93
	Adult Male	0.98	6.59
Kubu	Juvenile Female	NA	NA
	Juvenile Male	18.80	18.80
	Adult Female	0.25	31.75
	Adult Male	10.61	10.61
Lemontree	Juvenile Female	0.25	3.38
	Juvenile Male	2.06	17.30
	Adult Female	2.44	4.84
	Adult Male	1.56	29.94
Noha	Juvenile Female	1.39	5.25
	Juvenile Male	3.44	3.44
	Adult Female	26.81	26.81
	Adult Male	5.02	5.45

Table. S7: Ethogram explaining the definitions of recorded exploration events, divided in two explorative events: mouth exploration (grey) and hand exploration (white).

Exploration event	**Definition**
Smell	A smell event was recorded every time a monkey put its nose in close contact (< 10 cm) to one of the metal box.
Bite	Biting was defined each time a monkey open the mouth in contact with the metal box.
Taste	Taste event was recorded every time a monkey put his lips in contact with the metal box.
Grabbing	Grabbing was recorded every time a monkey stood up bipedal and grab the box with both hands.
Play	A play event was recorded every time a monkey grab or touch one of the hooks (used in captivity to attach the box to the fence)
Touch	A touch event was recorded every time a monkey physically touched the metal box with its hand or feet.

Touch screen	A touch event was recorded every time a monkey physically touched the screen.

Table. S8: Number of hand and mouth explorative behaviours for each group. Minimum and maximum behaviours are shown.

Context	**Group**	**Minimum Total hand exploration**	**Maximum Total mouth exploration**
Wild	Ankhase	23	7
	Baie Dankie	33	15
	Kubu	63	18
	Lemontree	176	20
	Noha	48	10
Sanctuary	Boeta	27	28
	Liffie	47	19
	Poena	130	22

Table. S9: Number of hand and mouth explorative behaviours for each individual. Minimum and maximum behaviours are shown.

Context	**Group**	**Age and Sex classes**	**Minimum Total hand exploration**	**Maximum Total mouth exploration**
Wild	Ankhase	Juvenile Female	1	3
		Juvenile Male	3	4
		Adult Female	23	9
		Adult Male	NA	NA
	Baie Dankie	Juvenile Female	6	6
		Juvenile Male	8	4
		Adult Female	33	15
		Adult Male	4	6
	Kubu	Juvenile Female	NA	NA
		Juvenile Male	3	6
		Adult Female	63	18
		Adult Male	9	11
	Lemontree	Juvenile Female	10	8
		Juvenile Male	20	8
		Adult Female	11	10
		Adult Male	176	20
	Noha	Juvenile Female	5	3
		Juvenile Male	1	5
		Adult Female	48	10
		Adult Male	5	9

4.2 Supplemental Information Chapter 2

Table. S1: Demographic details of the eight groups in the sanctuary and wild contexts. Group composition varied over the course of the study, so minimum and maximum counts are shown.

Context	Group	Age and Sex Classes	Minimum count	Maximum count
Wild	Ankhase	Adult Female	7	8
		Adult Male	2	6
		Juvenile Female	3	4
		Juvenile Male	7	10
	Baie Dankie	Adult Female	19	23
		Adult Male	9	12
		Juvenile Female	9	16
		Juvenile Male	14	18
	Kubu	Adult Female	2	4
		Adult Male	1	3
		Juvenile Female	6	7
		Juvenile Male	4	6
	Noha	Adult Female	10	15
		Adult Male	5	7
		Juvenile Female	7	10
		Juvenile Male	7	12
Sanctuary	Boeta	Adult Female	1	1
		Adult Male	2	2
		Juvenile Female	0	0
		Juvenile Male	0	0
	Cowen	Adult Female	1	2
		Adult Male	0	0
		Juvenile Female	2	4
		Juvenile Male	6	14
	Liffie	Adult Female	1	1
		Adult Male	1	1
		Juvenile Female	8	10
		Juvenile Male	11	12

Poena	Adult Female	1	3
	Adult Male	1	4
	Juvenile Female	2	5
	Juvenile Male	7	11

Table. S2: The count of available demographics in each context, with the count of individuals which participated at least once.

Context	**Age and Sex Classes**	**Available**	**Participating**	**Percentage participating**
Wild	Juvenile Female	43	20	46.51%
	Juvenile Male	56	31	55.36%
	Adult Female	53	28	52.83%
	Adult Male	40	22	55.00%
Sanctuary	Juvenile Female	22	13	59.09%
	Juvenile Male	37	30	81.08%
	Adult Female	7	5	71.43%
	Adult Male	7	5	71.43%

Table. S3: Group sizes throughout testing period.

Context	**Group**	**Minimum group size**	**Maximum group size**
Wild	Ankhase	23	26
	Baie Dankie	57	65
	Kubu	15	18
	Noha	32	40
Sanctuary	Boeta	3	3
	Cowen	10	18
	Liffie	21	22
	Poena	11	18

Table. S4: The number of test sessions conducted in each context (split by Group).

Context	**Group**	**Total test sessions**	**Total uninterrupted test sessions**
Wild	Ankhase	62	57
	Baie Dankie	55	49
	Kubu	54	49
	Noha	111	99
Sanctuary	Boeta	160	146
	Cowen	55	46
	Liffie	99	90
	Poena	143	120

Table. S5: Total presentation time per Group.

Context	**Group**	**Total presentation time (hours)**
Wild	Ankhase	75.3
	Baie Dankie	50.3
	Kubu	53.1
	Noha	115.0
Sanctuary	Boeta	78.9
	Cowen	27.8
	Liffie	51.7
	Poena	66.9

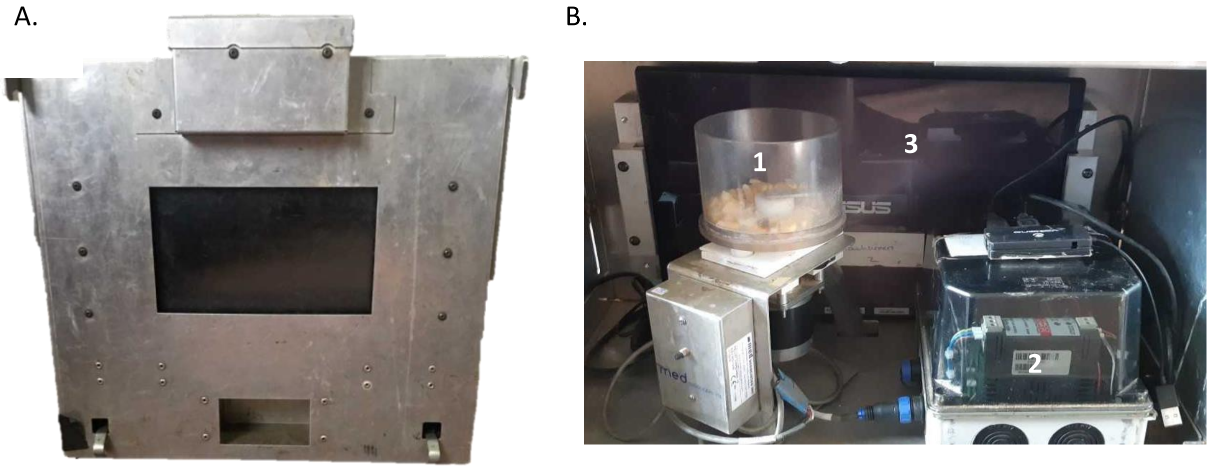


Figure. S1: a) the portable touchscreen and b) its components. a) the metal box from the point of view of monkeys, with four hooks, two lower and two upper hooks used to attach the system to the fence of enclosures at the sanctuary. b) the components of the portable touchscreen: 1) food dispenser, 2) electronic control unit, 3) touch frame infrared panel, all connected by USB hub to the convertible laptop.

*4.2.1 Additional information: ZACI (**Z**oo-based **A**nimal-**C**omputer-**I**nteraction System)*

The ZACI is composed of a waterproof aluminium casing (45 cm x 50 cm x 26 cm, HxWxD) manufactured by Autz & Herrmann GmbH, Heidelberg. Inside the casing, there is a touch panel to protect the laptop from damage and dirt surrounded by a 15.6 infrared touchframe to register touches. For each touch, the infrared sends the information to a convertible laptop (HP ENVY, running Microsoft Windows).

4.2.2 Description of cognitive tasks

Task 1 (Habituation phase): A blue square was presented in the centre of the screen, with a white background. Monkeys received a reward if they touched any location on the screen, either on the blue square or outside the blue square. Once the subject stayed in front of the screen and interacted with the touchscreen repeatedly, we considered this first habituation phase completed.

Task 2: The same image (central blue square on a white background) was presented on the screen, but in this phase, monkeys were rewarded only when they touched the blue square.

Task 3: The blue square changed position each time the monkey touched the square. To pass this task, we used the same criterion as in Task 2.

We tested monkeys that reached criterion on the three training tasks with a Classical Associative Learning task (CAL) and a Reversal Classical Associative Learning task (RCAL). We showed two stimuli on the screen simultaneously. One of the stimuli was associated with rewards (correct) and the other was unrewarded and simply followed by another trial (incorrect). This CAL task aimed to test the ability of individuals to successfully discriminate between the two stimuli. To avoid any possible preference for certain stimuli, we used different stimuli for each group: NH and Boeta had a yellow triangle with black stripes (correct) displayed with a purple circle with white spots (incorrect); BD and Cowen had the same stimuli but with the rewarded stimuli reversed; AK and Poena had an orange triangle with white spots (incorrect) and a dark green circle with black stripes (correct). In RCAL we studied individuals' cognitive flexibility by requiring them to select the previously unrewarded stimulus. To present the RCAL we reversed all stimuli once individuals reached the same criterion in the CAL task as in Task 2 and Task 3.

4.2.3 Data analysis

Model assessment

All full models were compared with either null models including only the random effects structure or intercept-only null models, using likelihood ratio tests (function anova in R with test set to "Chisq"). For GLMMs, collinearity was assessed using Variance Inflation Factors (function 'vif' in the R package car; Fox et al., 2012). Variance inflation factors below five were considered acceptable. Where relevant (for models with poisson, generalized poisson, or negative binomial distributions), overdispersion was assessed using the 'testDispersion' function in the R package DHARMa (Hartig, 2020). Model predictions (estimated marginal means) were generated using the function 'ggemmeans' in the R package ggeffects (Lüdecke, 2018). Full-null model comparison was also used to assess the Cox proportional hazards model, and for this model the assumption of proportional hazards was tested using the function "cox.zph" from the R package 'survival' (Therneau, 2022). The assumption was met by all variables in the model as well as globally.

Table. S6: Model output GLMM 6, Trials required to pass Task 3.

Note: This model was not a significantly better fit to the data than a null model containing only the random effect of Group.

Effect	**Estimate**	**Wald 95% confidence interval**	**p-value**
Intercept	5.25	4.85; 5.66	
Context (Sanctuary)	0.32	-0.25; 0.89	0.27

Additional analyses

Number of individuals participating per session in wild groups

To explore whether there were group differences in the number of individuals participating in each testing session between the wild groups, we used a generalized linear model with a poisson distribution. The outcome variable was the number of individuals participating in the task in a given session. Session Duration (z-transformed) and Group were included as predictor variables. As Session Durations were generally dictated by the ongoing interest of individuals to participate, this variable was included as a control variable rather than as a variable of interest.

This model was a significantly better fit to the data than an intercept-only null model ($\chi^2 = 120.37$, $p < 0.0001$; see Table. S8 for model output). There was a significant effect of Group upon the number of individuals participating in each session (overall significance calculated using the 'Anova' function in the package 'car': $\chi^2 = 16.15$, $p = 0.001$). A post-hoc Tukey test revealed that significantly fewer individuals participated per session in Kubu than in Baie Dankie ($\beta = -0.35$, $p < 0.001$). There were no other significant differences between the groups (see Figure. S2).

Table. S7: Results of a GLMM predicting the number of individuals participating per session across the four wild groups.

Effect	**Estimate**	**Wald 95% confidence interval**	**p-value**
Intercept	1.63	1.53; 1.74	
Session duration (z-transformed)	0.25	0.21; 0.30	< 0.0001
Group BD	0.16	0.00; 0.31	0.049
Group KB	-0.19	-0.36; -0.02	0.026
Group NH	-0.01	-0.14; 0.13	0.928

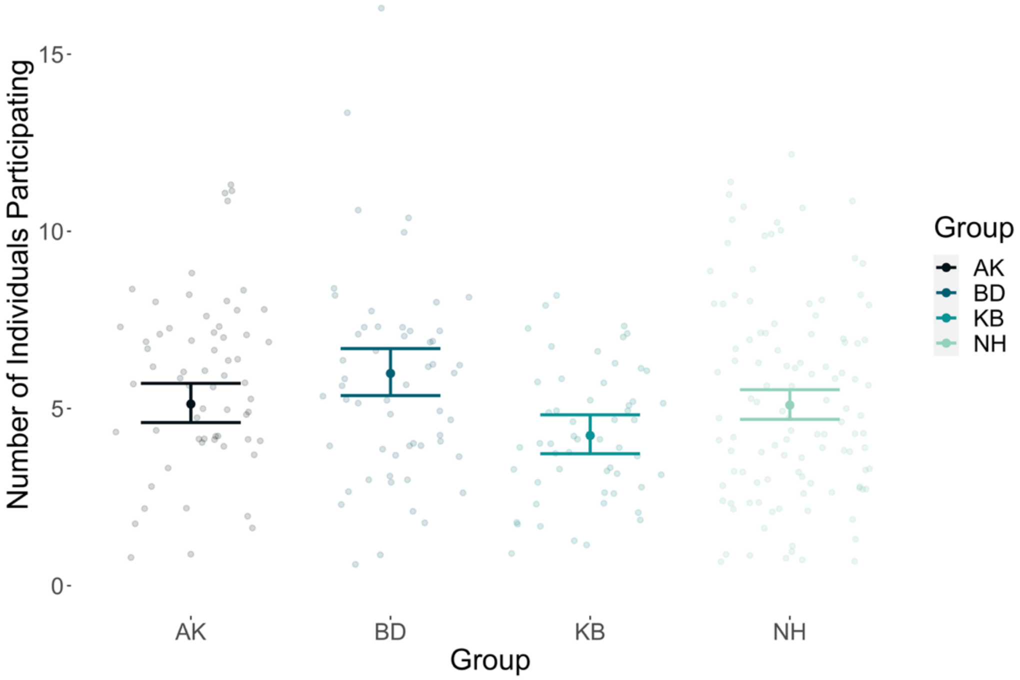


Figure. S2: The number of individuals participating per session in each of the four wild groups tested. Model predictions (estimated marginal means) of the effect of Group on number of individuals participating are shown by solid points, with error bars showing the 95% confidence interval. Lighter points show the observed number of individuals participating per session.

Impact of previous success on participation in the wild population

The effect of previous success on wild individuals' likelihood of participation in the next test session was analysed using a binomial GLMM. Age Class, Sex, Group and Session Duration (z-transformed) were included as predictors, with an interaction between Age Class and Sex, and a random effect of Individual. The effect of previous success was analysed by including as a predictor variable the number of rewards an individual had received the previous time they participated, with this value resetting to NA if more than 30 days had passed since the group had received the touchscreen. As only individuals who had interacted with the touchscreen at least once had a previous reward value, the sample size for this analysis was limited to 94 individuals.

The full model (Analysis 4) was a significantly better fit to the data than a null model containing only the random effects structure ($\chi^2 = 205.35$, $p < 0.0001$). As in the previous analysis of likelihood of participation in the task, there was a significant interaction between Sex and Age Class (Table. 5), with adult males being significantly less likely to participate than juvenile males ($\beta = -1.83$, $p = 0.0002$), while in this model age class did not influence female participation ($\beta = -0.06$, $p = 0.83$) – note that this may be due to the reduced sample used for this analysis, which could only include individuals who participated at least once in the task. The variable of interest in this model, previous success, had a significant influence on the likelihood of participation ($\beta = 0.37$, $p < 0.0001$, see Figure. 6), with individuals being more likely to participate the more rewards they had received the last time they participated.

Table. S8: Results of a GLMM predicting the likelihood of participation by individuals per session in the task in the wild population, including the variable of interest: Previous Reward Count.

Effect	**Estimate**	**Wald 95% confidence interval**	***p*-value**
Intercept	-0.74	-1.67; 0.18	
Age Class (Adult)	-0.06	-0.50; 0.62	0.831
Sex (Male)	0.67	-0.15; 1.49	0.111
Previous Reward Count (z-transformed)	0.37	0.27; 0.47	< 0.0001
Group (Baie Dankie)	-0.77	-1.71; 0.17	0.110
Group (Kubu)	-0.50	-1.58; 0.58	0.365
Group (Noha)	-0.31	-1.23; 0.62	0.515
Session Duration (z-transformed)	0.40	0.32; 0.48	< 0.0001
Interaction: Age Class x Sex	-1.83	-2.79; -0.86	0.0002

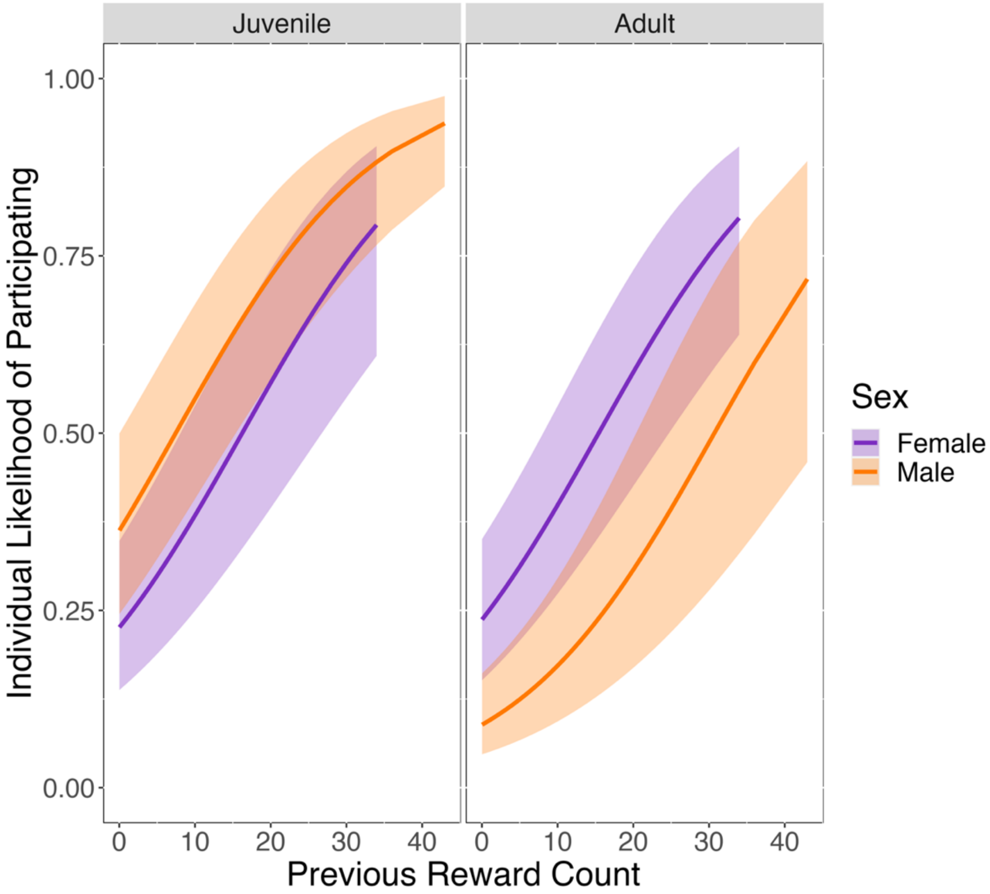


Figure. S3: Model predictions (estimated marginal means) of the effect of the number of Previous Rewards on the likelihood of participation in the task. The solid line shows the prediction for each Sex and Age Class, with shaded ribbons showing the 95% confidence interval.

Effect of breaks in testing

The length of time (in days) since the previous testing session was calculated for each testing session. This ranged from 0 (on the first day of testing in each group) to 426 days. Due to the COVID-19 pandemic, there were occasionally longer breaks in testing, meaning that the interval between test sessions ranged from zero to 310 days in the wild population, and one to 426 days in the sanctuary population. In order to test whether the length of time between experimental sessions impacted individuals' likelihood of participation, we used a binomial GLMM with individual participation as the outcome variable, and 'Time Since Previous Session' (measured in days and z-transformed), Context (Wild vs. Sanctuary) and Session Duration (z-transformed) as predictors, with random effects of Individual and Group. No significant interaction between Context and Time Since Previous Session was found, and so this interaction term was not included in the final model. This model was a significantly better fit to the data than a null model containing only the random effects ($\chi^2 = 281.17$, $p < 0.0001$). The length of time since the previous test session did not have a significant effect upon individuals' likelihood of participation (see Table. S8; Figure. S3).

Table. S9: Results of a GLMM modelling the impact of the time since previous session upon individuals' likelihood of participation.

Effect	**Estimate**	**Wald 95% confidence interval**	**p-value**
Intercept	-4.11	-4.84; -3.38	
Time Since Previous Session (z-transformed)	-0.03	-0.09; 0.03	0.282
Context (Sanctuary)	1.88	0.71; 3.04	0.002
Session Duration (z-transformed)	0.55	0.49; 0.62	< 0.0001

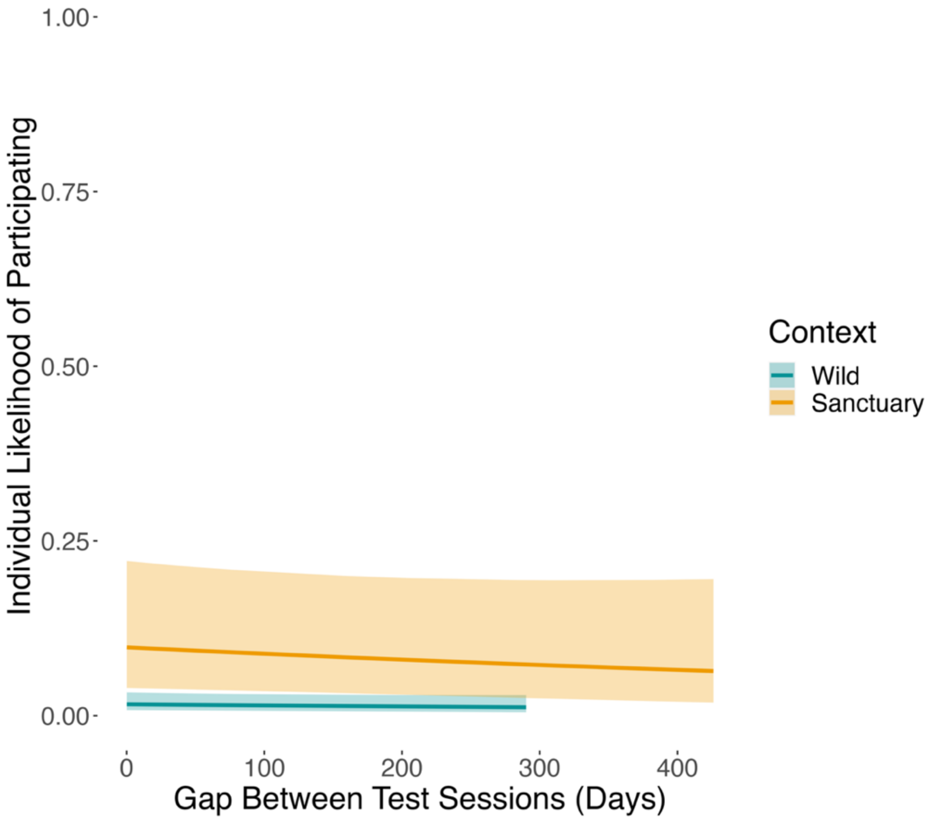


Figure. S4: Model predictions (estimated marginal means) of the effect of the length of time between test sessions upon the likelihood of participation in the task. The solid line shows the prediction for each Context (wild and sanctuary), with shaded ribbons showing the 95% confidence interval.

References

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., & Monette, G. (2012). Package ‘car’. *Vienna: R Foundation for Statistical Computing*, *16*.

Hartig, F. (2020). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3. 3.0. *Computer software https://CRAN. R-project. org/package= DHARMa*.

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772.

Therneau T (2022). *A Package for Survival Analysis in R*. R package version 3.4-0, https://CRAN.R-project.org/package=survival.

4.3 Supplemental information Chapter 3

Table. S1: Represents the description of 16 wild and 10 sanctuary individuals who has participate at least at one MTS or/and RTL experiments. In this table there are the details of Group, Sex and Age classes, Number of experiments in MTS and RLT and both sum of trials in MTS and RLT. In grey sanctuary monkeys and in white wild ones.

Individual	Group	Sex	Age	Total experiment MTS	Sum Trial MTS	Total experiment RLT	Sum Trial RLT
Gaya	Noha	F	Adult	6	50	9	88
Gilane	Ankhase	M	Juvenile	9	62	NA	NA
Ginqika	Ankhase	F	Adult	16	143	19	183
Granada	Noha	F	Adult	16	148	17	137
Griffin	Noha	M	Juvenile	8	66	NA	NA
Griselle	Noha	F	Juvenile	15	121	18	180
Guatemala	Noha	F	Adult	5	34	NA	NA
Nakoo	Ankhase	M	Juvenile	12	109	NA	NA
Ngenakubu	Ankhase	M	Juvenile	6	54	14	131
Obsessie	Baie Dankie	F	Juvenile	1	1	NA	NA
Oerwood	Baie Dankie	F	Adult	18	137	18	139
Oortjie	Baie Dankie	F	Adult	14	140	25	246
Opa	Baie Dankie	M	Juvenile	6	30	NA	NA
Pomelo	Baie Dankie	M	Juvenile	10	100	NA	NA
Pratella	Noha	F	Juvenile	21	185	NA	NA
Xiashan	Noha	M	Juvenile	20	225	NA	NA
Boeta	Boeta	M	Adult	8	78	17	151
Cowen	Cowen	F	Juvenile	7	70	15	141
Fanjan	Poena	M	Juvenile	5	49	7	63
Fielis	Boeta	M	Adult	4	35	13	118
Gyzmo	Poena	M	Juvenile	8	80	18	171
Jeff	Cowen	M	Juvenile	1	10	NA	NA
Jokie	Boeta	F	Adult	3	30	18	181
Nielsie	Cowen	M	Juvenile	6	59	NA	NA
Poena	Poena	F	Adult	8	80	11	105
Rainbow	Cowen	F	Adult	7	61	NA	NA

Table. S2: Represents the description of 25 individuals who interacted at least once with the MTS. In this table there are the description of Group, Context, Sex, Age, Part of the body, and the percentage of part of the body used while playing the Matching to sample test. In grey sanctuary monkeys and in white wild ones. In addition, three individuals in red have been removed from the analysis.

Individual	**Group**	**Context**	**Sex**	**Age**	**Part of the body**	**% Part of body used during MTS**
Gaya	Noha	Wild	F	Adult	lefthand	54,7
Gaya	Noha	Wild	F	Adult	muzzle	19,8
Gaya	Noha	Wild	F	Adult	righthand	25,5
Gilane	Ankhase	Wild	M	Juvenile	lefthand	4,9
Gilane	Ankhase	Wild	M	Juvenile	muzzle	54,8
Gilane	Ankhase	Wild	M	Juvenile	righthand	40,3
Ginqika	Ankhase	Wild	F	Adult	lefthand	6,1
Ginqika	Ankhase	Wild	F	Adult	muzzle	60,1
Ginqika	Ankhase	Wild	F	Adult	righthand	33,8
Granada	Noha	Wild	F	Adult	lefthand	0,4
Granada	Noha	Wild	F	Adult	muzzle	1
Granada	Noha	Wild	F	Adult	righthand	98,6
Griffin	Noha	Wild	M	Juvenile	lefthand	34,8
Griffin	Noha	Wild	M	Juvenile	muzzle	31,8
Griffin	Noha	Wild	M	Juvenile	righthand	33,4
Griselle	Noha	Wild	F	Juvenile	lefthand	7,8
Griselle	Noha	Wild	F	Juvenile	muzzle	82,2
Griselle	Noha	Wild	F	Juvenile	righthand	10
Guatemala	Noha	Wild	F	Adult	lefthand	11,8
Guatemala	Noha	Wild	F	Adult	muzzle	85,3
Guatemala	Noha	Wild	F	Adult	righthand	2,9
Nakoo	Ankhase	Wild	M	Juvenile	lefthand	76,2
Nakoo	Ankhase	Wild	M	Juvenile	muzzle	7,3
Nakoo	Ankhase	Wild	M	Juvenile	righthand	16,5
Ngenakubu	Ankhase	Wild	M	Juvenile	lefthand	13,5
Ngenakubu	Ankhase	Wild	M	Juvenile	muzzle	62,2
Ngenakubu	Ankhase	Wild	M	Juvenile	righthand	24,3
Oerwood	Baie Dankie	Wild	F	Adult	lefthand	8,6
Oerwood	Baie Dankie	Wild	F	Adult	muzzle	82,4
Oerwood	Baie Dankie	Wild	F	Adult	righthand	9
Oortjie	Baie Dankie	Wild	F	Adult	lefthand	0,3
Oortjie	Baie Dankie	Wild	F	Adult	muzzle	99,7
Oortjie	Baie Dankie	Wild	F	Adult	righthand	0
Opa	Baie Dankie	Wild	M	Juvenile	lefthand	33,3

Opa	Baie Dankie	Wild	M	Juvenile	muzzle	50
Opa	Baie Dankie	Wild	M	Juvenile	righthand	16,7
Pomelo	Baie Dankie	Wild	M	Juvenile	lefthand	21
Pomelo	Baie Dankie	Wild	M	Juvenile	muzzle	25
Pomelo	Baie Dankie	Wild	M	Juvenile	righthand	54
Pratella	Noha	Wild	F	Juvenile	lefthand	25,9
Pratella	Noha	Wild	F	Juvenile	muzzle	40,5
Pratella	Noha	Wild	F	Juvenile	righthand	33,6
Xiashan	Noha	Wild	M	Juvenile	lefthand	56,6
Xiashan	Noha	Wild	M	Juvenile	muzzle	9,4
Xiashan	Noha	Wild	M	Juvenile	righthand	34
Boeta	Boeta	Sanctuary	M	Adult	lefthand	21,8
Boeta	Boeta	Sanctuary	M	Adult	muzzle	12,3
Boeta	Boeta	Sanctuary	M	Adult	righthand	65,9
Cowen	Cowen	Sanctuary	F	Juvenile	lefthand	34,6
Cowen	Cowen	Sanctuary	F	Juvenile	muzzle	9,5
Cowen	Cowen	Sanctuary	F	Juvenile	righthand	55,9
Fanjan	Poena	Sanctuary	M	Juvenile	lefthand	13,4
Fanjan	Poena	Sanctuary	M	Juvenile	muzzle	25
Fanjan	Poena	Sanctuary	M	Juvenile	righthand	61,6
Fielis	Boeta	Sanctuary	M	Adult	lefthand	36,2
Fielis	Boeta	Sanctuary	M	Adult	muzzle	7,2
Fielis	Boeta	Sanctuary	M	Adult	righthand	56,6
Gyzmo	Poena	Sanctuary	M	Juvenile	lefthand	58,7
Gyzmo	Poena	Sanctuary	M	Juvenile	muzzle	0
Gyzmo	Poena	Sanctuary	M	Juvenile	righthand	41,3
Jeff	Cowen	Sanctuary	M	Juvenile	lefthand	20
Jeff	Cowen	Sanctuary	M	Juvenile	muzzle	0
Jeff	Cowen	Sanctuary	M	Juvenile	righthand	80
Jokie	Boeta	Sanctuary	F	Adult	lefthand	39,4
Jokie	Boeta	Sanctuary	F	Adult	muzzle	1,4
Jokie	Boeta	Sanctuary	F	Adult	righthand	59,2
Nielsie	Cowen	Sanctuary	M	Juvenile	lefthand	30,5
Nielsie	Cowen	Sanctuary	M	Juvenile	muzzle	22
Nielsie	Cowen	Sanctuary	M	Juvenile	righthand	47,5
Poena	Poena	Sanctuary	F	Adult	lefthand	23,6
Poena	Poena	Sanctuary	F	Adult	muzzle	0,4
Poena	Poena	Sanctuary	F	Adult	righthand	76
Rainbow	Cowen	Sanctuary	F	Adult	lefthand	31,1
Rainbow	Cowen	Sanctuary	F	Adult	muzzle	9,8

Rainbow	Cowen	Sanctuary	F	Adult	righthand	59,1

Table. S3: Represent results of post hoc Tukey test predicting the number of touches taken by individual using different part of the body (Muzzle, right hand, left hand).

	Estimate	**Std. Error**	**z value**	**p-value**
Muzzle - lefthand == 0	-0.24297	0.12385	-1.962	0.12132
righthand - lefthand == 0	0.08719	0.11650	0.748	0.73398
righthand - Muzzle == 0	0.33016	0.10888	3.032	**0.00685 ****

Table. S4: Represent results of post hoc Tukey test predicting the interaction between number of touches taken by individual using different part of the body (Muzzle, Right hand, Left hand) when correct stimulus was on the right and left side of the screen.

Contrast	**odds.ratio**	**SE**	**z.ratio**	**p-value**
left lefthand / right lefthand	0.733	0.1380	-1.647	0.5669
left lefthand / left Muzzle	0.715	0.1293	-1.857	0.4292
left lefthand / right Muzzle	0.938	0.1617	-0.369	0.9991
left lefthand / left Righthand	0.941	0.1699	-0.339	0.9994
left lefthand / right Righthand	0.589	0.1051	-2.966	0.0358
right lefthand / left Muzzle	0.974	0.1658	-0.152	1.0000
right lefthand / right Muzzle	1.279	0.2060	1.531	0.6443
right lefthand / left Righthand	1.282	0.2180	1.464	0.6876
right lefthand / right Righthand	0.803	0.1346	-1.308	0.7807
left Muzzle / right Muzzle	1.313	0.2001	1.787	0.4743
left Muzzle / left Righthand	1.316	0.2130	1.697	0.5338
left Muzzle / right Righthand	0.824	0.1313	-1.213	0.8308
right Muzzle / left Righthand	1.002	0.1525	0.015	1.0000
right Muzzle / right Righthand	0.628	0.0938	-3.115	0.0227
left Righthand / right Righthand	0.626	0.0996	-2.941	0.0384

Animal Cognition
https://doi.org/10.1007/s10071-021-01589-y

ORIGINAL PAPER

Captivity and habituation to humans raise curiosity in vervet monkeys

Sofia Ingrid Fredrika Forss[1,2,3] · **Alba Motes-Rodrigo**[1,4] · **Pooja Dongre**[1,2] · **Tecla Mohr**[1,2] · **Erica van de Waal**[1,2]

Received: 30 June 2021 / Revised: 29 September 2021 / Accepted: 27 November 2021

Abstract

The cognitive mechanisms causing intraspecific behavioural differences between wild and captive animals remain poorly understood. Although diminished neophobia, resulting from a safer environment and more "*free*" time, has been proposed to underlie these differences among settings, less is known about how captivity influences exploration tendency. Here, we refer to the combination of reduced neophobia and increased interest in exploring novelty as "*curiosity*", which we systematically compared across seven groups of captive and wild vervet monkeys (*Chlorocebus pygerythrus*) by exposing them to a test battery of eight novel stimuli. In the wild sample, we included both monkeys habituated to human presence and unhabituated individuals filmed using motion-triggered cameras. Results revealed clear differences in number of approaches to novel stimuli among captive, wild-habituated and wild-unhabituated monkeys. As foraging pressure and predation risks are assumed to be equal for all wild monkeys, our results do not support a relationship between curiosity and safety or free time. Instead, we propose "*the habituation hypothesis*" as an explanation of why well-habituated and captive monkeys both approached and explored novelty more than unhabituated individuals. We conclude that varying levels of human and/or human artefact habituation, rather than the risks present in natural environments, better explain variation in curiosity in our sample of vervet monkeys.

Keywords Curiosity · Novelty response · Neophobia · Exploration · Captivity effect · Captivity bias · Human habituation

Introduction

Due to both feasibility and logistics, most experimental work on animal cognition is performed in captivity. Nevertheless, cognitive experiments are increasingly being carried out with wild populations in ecologically relevant field settings (Morand-Ferron et al. 2011; van de Waal and Bshary 2011; Thornton and Samson 2012; Benson-Amram et al. 2013; Cauchard et al. 2013; Shaw et al. 2015; Rasolofoniaina et al. 2021). Field experiments usually present wild animals with novel problems in the form of puzzle boxes or devices made of anthropogenic materials. Despite habituation to the apparatuses over time, many studies point to individual differences in neophobia and motivation to participate rather than to differences in cognitive capacities between wild and captive individuals (Overington et al. 2011; Benson-Amram and Holekamp 2012; van Horik et al. 2017; Rössler et al. 2020; Martina et al. 2021). These results suggest that, to successfully implement comparisons of further cognitive skills among settings, we need to improve our understanding of how the motivation to interact and explore novelty differs between captive and wild individuals.

In the broadest sense, curiosity is described as "*the motivation to seek information about something unfamiliar*" (Berlyne 1950; Loewenstein 1994; Byrne 2013; Kidd and Hayden 2015; Gross et al. 2020). This 'novelty-seeking' is notably in the absence of any immediate external reward (Wang and Hayden 2019). In humans, psychologists commonly address curiosity through questionnaires and self-reports (see overview in Gross et al. 2020). In non-human animals, however, identifying curiosity requires measures of more specific behavioural components describing readiness and motivation to gather information about something

---

✉ Sofia Ingrid Fredrika Forss
sofia.forss@ieu.uzh.ch

[1] Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

[2] Inkawu Vervet Project, Mawana Game Reserve, KwaZulu Natal, Pretoria 3115, South Africa

[3] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zürich, Switzerland

[4] Department of Early Prehistory and Quaternary Ecology, Eberhard-Karls-Universität Tübingen, Tübingen, Germany

unfamiliar, outside the context of general survival activities (Mettke-Hofmann et al. 2002; Byrne 2013; Hall et al. 2018). Moreover, given the high risks present in most natural environments, many animals have intrinsically strong neophobia, potentially preventing them from engaging in novelty exploration (Barnett 1958; Greenberg 1990a; Mettke-Hofmann et al. 2002). Therefore, it is likely that overcoming neophobia is foundational for when and how wild animals can pursue curiosity driven exploration. Generally, the term neophobia is used to describe "*fear*" of novelty (Greenberg 1990a, b, 2003; Fox and Millam 2007; Greggor et al. 2016a, b), but since we cannot always infer fearful emotions of animals from novel-object test paradigms, the more commonly used definition is "*novelty avoidance*" (Misslin and Cigrang 1986; Benson-Amram et al. 2013; Forss et al. 2015; Greggor et al. 2015; Rasolofoniaina et al. 2021). The contrasting response of closely approaching novel stimuli or preferring novelty over familiarity is termed neophilia (Day et al. 2003; Greenberg 2003; Kaulfuß and Mills 2008). Crucially, one needs to keep in mind that being explorative is *not* the opposite of being neophobic. Instead, explorative behaviours encompass multiple motivational actions relevant to gain information about something unfamiliar (Greenberg 2003; Biondi et al. 2010; Carter et al. 2012; Forss et al. 2017). Therefore, an animal can be both neophobic and simultaneously have a strong exploration tendency (Moretti et al. 2015; Forss et al. 2017). Here, we refer to curiosity as a positive response to novel stimuli expressed through the *combination* of low neophobia (measured as readiness to approach something new) and subsequent explorative behaviours used by an individual to gather knowledge of new encountered stimuli (measured as exploration events, e.g., handling, sniffing, etc.) (Damerius et al. 2017a).

One extreme case leading to reduced neophobia is the risk-free existence of captive animals (Barnett 1958; Brown et al. 2013). The "*captivity effect*" or "*captivity bias*" refers to measurable intra-species cognitive differences between individuals from natural and captive environments (Haslam 2013; Forss et al. 2015; van Schaik et al. 2016; Rössler et al. 2020). Beyond neophobia, a captivity effect has also been described for other behaviours like innovation (Benson-Amram et al. 2013; Rössler et al. 2020) and tool use (Kummer and Goodall 1985; Gruber et al. 2010; Shumaker et al. 2011; Haslam 2013). Variation in activity budgets between wild and captive animals (Veasey et al. 1996; Yamanashi and Hayashi 2011) forms the foundation of the argument that the captivity effect results from wild animals being more occupied with foraging and predator vigilance than captive conspecifics (Kummer and Goodall 1985; Brown et al. 2013; Amici et al. 2020). Accordingly, "*the free time hypothesis*" and "*the excess energy hypothesis*" propose that captive animals have a surplus of energy and a lower cognitive load allowing for higher levels of exploration and innovativeness than wild conspecifics, who are occupied searching for food, mating partners, or shelter (Kummer and Goodall 1985; Laidre 2008a; McCune et al. 2019; Amici et al. 2020). For example, captive hyenas (*Crocuta crocuta*) are less neophobic and more explorative than wild conspecifics, thereby outperforming them in certain problem-solving tasks (Benson-Amram et al. 2013). On the other hand, wild Mexican jays (*Aphelocoma wollweberi*) were faster problem-solvers than captive conspecifics (McCune et al. 2019) and wild-caught and laboratory raised Goffins cockatoos (*Cacatua goffiniana*) differed mainly in their motivation to *participate* in an experimental task, but not in their innovation rates (Rössler et al. 2020). Yet, if and what elements of captive life increase exploration tendencies is less clear. Findings from both primates and birds suggest that frequent exposure to human-made artefacts increases task performance as a result of habituation to artificial materials (Gajdon et al. 2004; Laidre 2008b; van de Waal and Bshary 2011; Damerius et al. 2017a, b). In some primate species, like the great apes, neophobia towards novelty is so high that it can be challenging to perform cognitive tasks through presentation of anthropogenic materials in their natural habitats (Forss et al. 2015; Kalan et al. 2019). Despite being exposed to novel objects for multiple months, wild orangutans (*Pongo abelii* and *Pongo pygmaeus*) only explored them on the rare occasions when they first observed a familiar human interact with the objects (i.e., human presence induced a curious response) (Forss et al. 2015). In captive orangutans, researchers found that individuals' degree of human orientation was positively correlated with exploration tendency, which in turn enhance their problem-solving skills (Damerius et al. 2017b). Thus, it is likely that, in some species, the captivity effect results from human habituation; captive animals show lower neophobia due to reduced risk perception regarding humans, and they develop stronger interest in novelty following increased experience with anthropogenic artefacts (van de Waal and Bshary 2011; Damerius et al. 2017a, b).

In the present study, we examined the foundations of curiosity by investigating neophobia and exploration tendencies in wild and captive vervet monkeys (*Chlorocebus pygerythrus*), using both novel-food and novel-object paradigms. Vervet monkeys are a particularly interesting species to address curiosity as they are opportunistic foragers and successfully inhabit anthropogenic environments like agricultural and urban areas, where they frequently exploit human food sources (Wimberger and Downs 2010; Thatcher et al. 2019). As a highly generalist and "nuisance" species, we expect them to show low levels of neophobia and high exploratory tendencies towards novel stimuli (Greenberg 2003; Sol et al. 2011; Tryjanowski et al. 2016; Griffin et al. 2017; Barrett et al 2019; Jarjour et al. 2020).

Specifically, we aimed to investigate whether curiosity in vervet monkeys is related to habituation to humans or due to low environmental risk and increased free time per se. In the first case, we compared the responses to novel stimuli of captive monkeys to those of wild habituated and wild unhabituated individuals. We predicted that if there existed a captivity effect, wild monkeys (habituated and unhabituated) would show less interest in unfamiliar objects and foods than captive conspecifics. To address the influence of human habituation on curiosity, we performed a separate test to compute the habituation index of each habituated vervet group. We predicted that groups with higher habituation indices would show more curious responses towards the battery of novel stimuli. In addition, for the wild-habituated monkeys, we evaluated whether the habitat structure of the location where the experiments were conducted had any influence on the monkeys' responses. Here, our prediction was that certain habitat structures, like high grass or open savannah, possibly impose higher predation risk and that monkeys would therefore be less motivated to explore in these habitat structures, compared to when the experiments were performed underneath a tree, providing a more protected location. Because sociality is expected to reduce risk perception and the presence of group members has been shown to increase approaches to novel objects in other species (Stöwe et al. 2006; Moretti et al. 2015; Forss et al. 2017), we predicted that in riskier habitat structures, monkeys would approach more in a social context, accompanied by one or more group members. Finally, given that captive and wild monkeys vary in their experiences with human-made artefacts, we used foods and objects of natural and artificial characteristics to evaluate any potential effect of stimuli features.

Methods

Subjects and study sites

We collected data on wild vervet monkeys (*Chlorocebus pygerythrus*) during February and March 2020 at the Inkawu Vervet Project (IVP) field site, located in Mawana game reserve (28° 00.327 S, 031° 12.348 E) in KwaZulu-Natal, South Africa. The study site is home to multiple wild groups of vervet monkeys, six of which are habituated to humans, regularly observed by researchers, and partake in experimental studies. Our data set comprised four of these groups, three of which are habituated since 2010 (Baie Dankie: $N=57$, Noha: $N=39$, Lemon Tree: $N=24$) and the fourth since 2013 (Kubu: $N=19$). In addition, the study area sustains at least three unhabituated groups, with many more living throughout the rest of the reserve. To enable data collection on unhabituated monkeys and to record any potential interactions with the novel stimuli, we placed motion-triggered video camera traps below two known sleeping trees of an unhabituated group (Congo: $N=11$).

We collected data on the captive population in March 2020 at the Wild Animal Trauma Centre & Haven (WATCH) vervet sanctuary, in Vryheid, KwaZulu Natal, South Africa. At the time of data collection, the WATCH sanctuary housed three groups of vervet monkeys. For logistical reasons, we only included two groups in our study (Poena: $N=17$ and Boeta: $N=3$). Most of the monkeys arrived at the sanctuary and were cared for by humans, since they were a few weeks old, and only a few individuals arrived at a later life stage. At first, infant monkeys arriving at a very young age are housed indoors and bottle nursed by human caretakers. Once they reach 3 months of age, they are slowly integrated into a group of conspecifics of mixed ages. Since the goal is to release these individuals back into their natural habitat (if circumstances allow), caretakers, and occasionally researchers, limit their contact with the monkey groups as much as possible.

Experimental setup

Habituated groups

We presented all four habituated groups with eight novel stimuli representing distinct materials, structures, and odours. We categorized four of these items as human-made or processed: boiled pasta (green, red, natural coloured), popcorn, toy mice (with Baldrian herb scent), and plastic toy cars (yellow, blue, green, and red). One item, white seashells, represented a completely natural occurring object. We chose the remaining three items to have "naturalistic features": fish (dead organic material in form of canned sardines), beef meatballs (raw organic material), and rubber butterflies of different colours (man-made material which mimics naturally occurring organisms) [Supplementary information (SI) Fig.S1]. We randomized the order of presentation of the novel stimuli across groups to avoid order effects and presented one type of novel stimulus at a time, on the ground, always with several items of each type to avoid potential monopolization by higher ranking group members. To attract the wild monkeys' attention to the experimental area, prior to the start of the experiment, we placed a handful of familiar food (corn) in the middle of the area where the novel items were spaced out. The habituated monkeys are used to eating corn as this food item has been introduced during both the habituation process as well as during previous experimental studies (van de Waal et al. 2013; van de Waal et al. 2017). Our main goal was to record any potential behavioural reactions towards the novel stimuli after the monkeys had been attracted to the area (within 20 m) and thus seen the novel stimuli. We did all experiments during the early mornings 1–2 h after dawn and we presented only one category of novel stimuli per group per day. We video recorded all experiments with Sony handycams HDR-CX200, two mounted on tripods from different angles, and a third that was handheld by an observer zooming in on any observed explorative behaviours. We presented all novel stimuli to the monkeys for 20 min, to allow enough time for lower ranking individuals to also approach in case the most dominant individuals were present at the start of the experiment preventing the lower rankers from approaching. Because the microhabitats vary slightly across groups as well as within each groups' home range, depending on their location on the day of our experiments, we categorized each experimental setup into three distinct habitat structures: open savannah (no canopy protection and no high grass), high grass (high grass but no canopy protection), and below tree (the experimental area was protected by canopy). In the open savannah, vervet monkeys are exposed to aerial predators like eagles and monkeys are observed to restrict their movement in high grass as the study area is home to a high abundance of pythons, capable of capturing vervet monkeys. Consequently, below trees represents the safest habitat structure for the monkeys as the tree canopy serves as protection from aerial predators and these areas do not have high grass.

Unhabituated group

The unhabituated group would not tolerate any human presence, as individuals from this group run away when human observers approach. They were however already habituated to eat corn when placed out in their habitat. We used an identical set up as with the habituated group, where we placed a small amount of corn in the middle of the area with the novel items. To record data from the unhabituated group, we placed the video camera traps in a way that they captured two different angles of the novel items, which we presented to the monkeys below two of their known sleeping trees. We used all the same novel stimuli as those used for the habituated groups. Because of the uncertainty regarding when the group would pass by the experimental location or when the monkeys would exactly use those sleeping trees, we presented the novel stimuli for 2 days in a row (unless a recording of any approaches by the group took place before the end of 2 consecutive days). Recordings from the camera traps thus allowed us to distinguish whether the group approached the novel stimuli on a single or multiple visits. For comparisons with the other group types, we only used the responses observed during the first visit.

Captive groups

At the WATCH sanctuary, we placed the novel stimuli in the main enclosure of the monkeys, who we moved into a side enclosure during the preparation of the experiment, and then let back into their normal enclosure. We used the same experimental protocol as for the habituated groups, including categories and numbers of novel stimuli, experimental duration, video camera placements, and recordings. As the captive monkeys were not used to corn, we used a few peanuts instead as the familiar food that would attract their attention to the experimental area.

Video coding and measurements

We coded all behavioural responses from video recordings. We recorded the number of close proximity approaches—those made to within 1 m of any of the multiple novel stimuli (food or item)—by any monkey that was present within a 20-m radius of the experimental location. As we defined a close proximity approach as each time a monkey approached within 1 m the novel stimuli, in any case where a monkey left the experimental area and then approached within 1 m again, this represented two approaches. For each approach that was made to the experimental area, we also distinguished whether or not the approach was made alone (when no other monkey was present within 1 m of the novel stimuli) or socially (when there was at least one other monkey present within 1 m of the novel stimuli). Once a monkey made physical contact with a novel item (0 m), we coded following exploration events: the number of smelling and tasting events, the number of times a monkey touched the novel item by hand, the number of times when a monkey chewed/bit the novel stimuli and the number of times a monkey lifted and moved an item. We then summed these behaviours into one exploration score labelled *number of exploration events* for each group and item. For each novel-food item, we additionally scored whether or not a monkey tasted it, defined as an event where a monkey licked a novel-food item, or every time a monkey put its lips onto a food item without ingesting it. All definitions of the coded behaviours as well as the frequencies of approaches and exploration events per group can be found in the ethogram in Table S1 and Fig. 4S in the Supplementary material.

Habituation test

To estimate the variation in human habituation among groups, we additionally performed a habituation test with the wild-habituated and captive groups. During this test, we exposed the monkeys to a human male that they had never seen before. The wild-habituated groups are familiar with researchers and project volunteers who attempt to distinguish themselves from other humans such as poachers by always wearing a turquoise blue cap while in the presence of the monkeys. In the habituation test, the man was dressed all in black clothes and wore a black cap. The man walked calmly towards the group of the monkeys shaking a Tupperware with corn as this is a familiar signal to the monkeys when they participate in research experiments. In the wild setting the man then placed the closed box with corn at his feet and as a group level habituation index, we measured the proportion of monkeys that approached the man to a distance of 1 m out of all the monkeys present within 20 m. In the captive setting, the man placed himself right at the enclosure mesh and placed peanuts right at his feet, which were in touchable distance to the monkeys. This test lasted 20 min in total.

Statistical analyses

We conducted the statistical analyses in R (version 3.6.1; R Core Team, 2020) and RStudio (version 1.2.5031; RStudio Team, 2020). We z-transformed covariates (habituation index and group size) to have a mean of zero and standard deviation of one before including them in the models to facilitate the interpretation of the coefficient estimates (Schielzeth 2010).

We first conducted a series of Spearman correlations to investigate whether any of the response measures (number of close proximity approaches, number of exploration events, and number of individuals within each group that tasted the food items) were correlated (Table 2). Since the number of individuals that tasted the different stimuli strongly correlated with the other response measures and this variable contained multiple missing values ($N=24$), we excluded this variable from further analysis.

To address the study aims, we fitted four different Generalized Linear Mixed Models (glmm) to the data (Table 1). We checked all models (Model 1a,1b, 2, 3) for overdispersion and overall stability (see Supplementary material) and z-transformed continuous variables (Habituation index and group size) before including them as fixed effects (Table 1). We draw inference by comparing the full model with a reduced (null) model lacking the predictors of interest but containing all other model elements (Forstmeier and Schielzeth 2011) using a likelihood ratio test (test “Chisq”' in the R function anova, (Dobson 2002). We implemented this approach to avoid “cryptic multiple testing” and to maintain type 1 error rates at the desired nominal level of 0.05 (Forstmeier and Schielzeth 2011). We calculated individual p values for each predictor using the function drop1 and R squared using the function r.squaredGLMM.

In the first model (Model 1a), we investigated the effects of group type (three levels: wild habituated, wild unhabituated, and captive) and stimuli type (8 levels, see above) on the number of approaches (response variable, count data) observed in a given group. For Model 1a, which had a Poisson error structure and log-link function, we fitted the

Table 1 Descriptions of the different model structures. Variables preceded by a “*z*” indicate that this variables were z-transformed before being introduced in the models

Model	Response variable	Fixed effects	Random effect	Offset
1a	Number of approaches	Stimuli type (8 levels); Group type (3 levels)	Group ID (7 levels)	Log group size
1	Number of approaches	Stimuli type (8 levels); Group type (2 levels)[a]; z-Habituation index	Group ID (6 levels)	Log group size
2	Number of exploratory events	Stimuli type (8 levels); Group type (2 levels)[a]; z-Habituation index	Group ID (6 levels)	Log group size
3	Two-column matrix including number of social approaches and number of individual approaches per trial	Stimuli type (8 levels); Habitat structure (3 levels); z-Habituation index; z-Group size[b]	Group ID (4 levels)[2]	–

Group size was log-transformed before being introduced as an offset

[a] Wild habituated groups were excluded from the model as they did not pose a habituation index

[b] Included as control predictor

Table 2 Coefficients and p values in parenthesis resulting from the correlation analyses performed among curiosity measures

	N approaches	*N* exploratory events	*N* tasting individuals
N approaches	1	0.47 (< 0.001)	0.45 (0.01)
N exploratory events	–	1	0.61 (< 0.001)
N tasting individuals	–	–	1

function glmer from the package lme4 (Bates et al. 2014). To account for group identity, we included the random intercept of group ID (7 levels, see above) into the model. We also included the logarithm of group size as an offset term to account for the different number of individuals in each of the groups.

To evaluate variation in close proximity approaches in relation to habituation level, we fitted a second model (Model 1b) using the same response variable, random structure, and the same offset as in Model 1a, but we changed the fixed effect structure. In addition to group type (2 levels: wild habituated and captive) and object type, we included the habituation index into Model 1b. As unhabituated groups did not have a habituation index, we excluded this group from those models where this variable was included (Model 1b and Model 2, see below).

In Model 2, we evaluated potential differences in explorative behaviour among the different group types (2 levels: wild habituated and captive), habituation level and stimuli type (8 levels). Similar to Models 1a and 1b, in Model 2, we included the random intercept of group ID as well as group size as an offset. To avoid overdispersion problems, we fitted this model using a quasi-Poisson model with a negative binomial distribution and the optimizer “bobyqa”.

In Model 3, we evaluated whether the proportion of social approaches varied according to habitat structure, habituation level, and stimuli type. In Model 3, we only included data from wild-habituated groups as these groups were the only ones that had been tested at locations with different habitat structures (below tree: $N = 14$, high grass: $N = 10$, and open savannah; $N = 13$). Model 3 was a binomial model with a response variable in the form of a matrix containing two columns corresponding to the number of social approaches and the number of individual approaches per trial (Baayen et al. 2008). Using such response variable, we account for the different number of approaches observed in different trials. Given that binomial models do not allow including offsets, we included group size as a control predictor. As before, we also included the random intercept of group ID was included in the model (although note that in this case group ID only had 4 levels, which is the threshold generally used to substitute a fixed by a random effect, meaning that it could have also been included as a control predictor).

Results

Relationship between response measurements

We found that all three response measures were significantly correlated among one another. The strongest correlation was found between the number of individuals tasting the novel stimuli and the number of exploratory events observed in a group. Correlation coefficients and p values of the correlations can be found in Table 2.

Factors influencing approaches to novel stimuli

Model 1a was overall significantly different from its corresponding null model (likelihood ratio test: $X^2 = 70.94$, df = 9, $p < 0.001$; R^2 full model = 0.5; SI: Table 3S). Group type and stimuli type both had significant effects on monkeys’ approaches to the novel stimuli (group type: df = 2, $p < 0.001$; stimuli type: df = 7, $p < 0.001$). More specifically, we found that the three group types significantly differed among them (Fig. 1), with captive groups presenting the highest average number of close approaches to the novel objects and foods (captive–wild habituated: $p < 0.001$, Hedge’s $g = 0.89$; captive–wild unhabituated: $p < 0.001$, Hedge’s $g = 1.16$; wild habituated–wild unhabituated: $p = 0.048$, Hedge’s $g = 2.23$).

The visualization of the effects of stimuli type on the number of approaches by group (SI: Fig. 2S) suggested that the differences among stimuli indicated by the model were driven by the high number of approaches in the largest captive group (Poena). To determine if this was the case, we fitted Model 1a again, but removed the data from the Poena group. In this case, we found that although the full-null model comparison was significant (likelihood ratio test: $X^2 = 20.92$, df = 9, $p = 0.013$; R^2 full model = 0.41) and the significant effect of group type remained ($p = 0.002$), stimuli type did not have a significant effect on the number of approaches ($p = 0.34$).

Model 1b (SI: Table 3S) was overall significant both when the Poena group was included and excluded (with

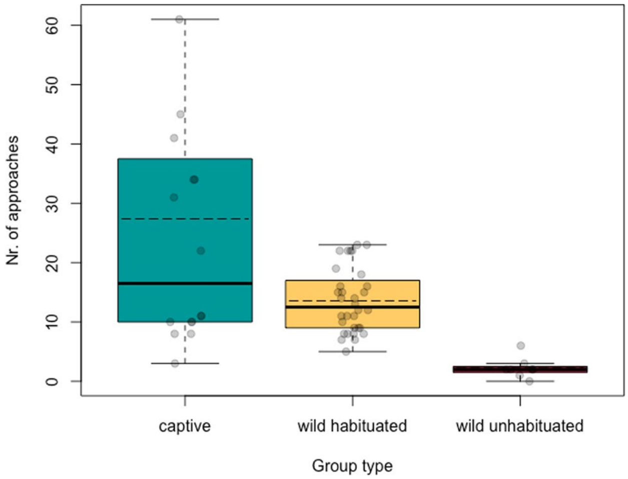


Fig. 1 Boxplots of the number of approaches performed by each group type. Each point corresponds to a trial ($N_{\text{captive}} = 16$, $N_{\text{wild habituated}} = 32$, $N_{\text{wild unhabituated}} = 8$). Dashed lines correspond to the group means and solid lines correspond to the group medians

Poena: likelihood ratio test: $X^2 = 66.83$, df = 9, $p < 0.001$; R^2 full model = 0.5; without Poena: likelihood ratio test: $X^2 = 18.18$, df = 9, $p = 0.03$; R^2 full model = 0.41). In neither case did the habituation index (with Poena: $p = 0.84$, without Poena: $p = 0.19$) nor the group type (with Poena: $p = 0.08$, without Poena: $p = 0.09$) have significant effects on the number of close approaches observed in the different groups.

Factors influencing exploration tendency

Model 2 was overall significant according to the full-null model comparison (likelihood ratio test: $X^2 = 67.28$, df = 9, $p < 0.001$; R^2 full model = 0.68, SI: Table 5S). All test predictors had a significant effect on the response (habituation index: $p < 0.001$, Fig. 2; stimuli type: $p = 0.001$), although the significance of group type (i.e., difference in exploration events between captive and wild-habituated groups) was marginal ($p = 0.047$, Hedge's $g = 0.58$). Visual assessment of the data suggested that the statistical differences in exploration tendency based on stimuli type were not driven by a particular group (SI: Fig. 3S). Differences in exploratory events based on stimuli type were investigated by changing the predictor's reference category (SI: Fig. 3S, Table 6S).

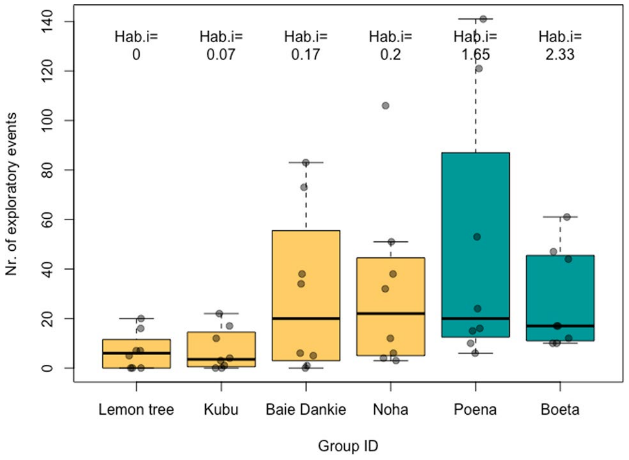


Fig. 2 Boxplots of the number of exploratory events observed in each of the groups. Hab.i represents the habituation index calculated for each group. Green boxes correspond to the captive groups and yellow boxes correspond to wild-habituated groups

Habitat structure and novelty approaches

Model 3 was overall significant according to the full-null model comparison (likelihood ratio test: $X^2 = 30.29$, df = 10, $p < 0.001$; R^2 full model = 0.68, SI: Table 7S). We found that the proportion of social approaches varied significantly across stimuli types ($p < 0.001$). However, the proportion of social approaches did not significantly differ based on habitat structure ($p = 0.47$, Fig. 3) or habituation index ($p = 0.99$).

Discussion

The effect of human habituation on curiosity

As opportunistic foragers, we would expect vervet monkeys to show relatively low neophobia to optimize their foraging niche (Greenberg and Mettke-Hofmann 2001; Greenberg 2003; Mettke-Hofmann 2014; Barrett et al. 2019). Our results, however, showed that within this species, neophobia

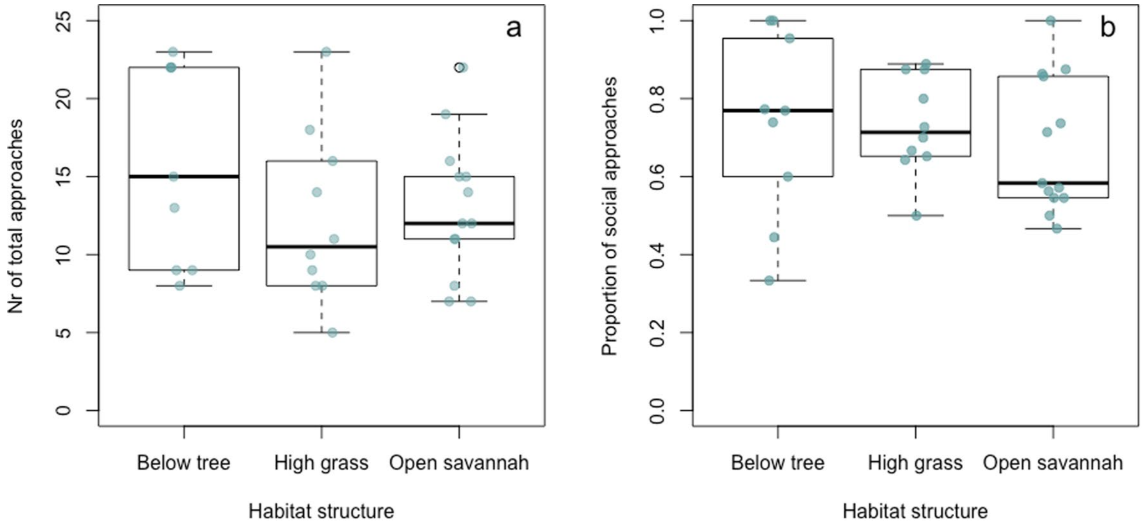


Fig. 3 **a** Boxplots of the number of total close approaches observed in the different habitat structures and **b** the proportion of social approaches out of the total number of approaches (individual and social) observed in each of the experimental locations featuring different habitat structures. Each dot corresponds to a trial

levels were conditional on environment (captive and wild) and habituation level (Fig. 1). Wild individuals approached novel stimuli significantly less than captive conspecifics and, as predicted, within the wild sample, unhabituated monkeys approached novel items less than habituated individuals (Fig. 1). This contrasts with both the "*free time*" and "*excess energy*" hypotheses (Kummer and Goodall 1985; Laland and Reader 1999; Reader and Laland 2001; Amici et al. 2020), which would predict that both types of wild vervet groups (habituated and unhabituated) have similar approach frequencies, since they live in the same environment and therefore experience similar predation pressure, food abundance, and presumably are in need for similar amount of foraging and vigilance activities. Moreover, we exposed the wild unhabituated group to the novel stimuli longer than the habituated monkeys, due to the setup by the video camera traps. Thus, the need for wild individuals to attend to other activities during the experiments cannot account for the observed differences in the number of approaches between these group types. As such, our data do not support the "*free time*" or "*excess energy hypotheses*". Rather, we propose *the habituation hypothesis* as a possible explanation of our findings, and discuss this more below.

Besides differences in the number of close approaches between monkeys from captive and wild habitats, the wild-habituated monkeys made an intermediate number of approaches, in-between their captive and wild unhabituated conspecifics (Fig. 1). The captive monkeys in our sample had never (or only at very early age) experienced any negative reinforcement when approaching anything unfamiliar as they spent all their life within a risk-free, food provisioned habitat and thereby probably have a positive perception of humans. This experience was reflected in the results of the habituation test, as almost all captive monkeys approached the man to the closest possible distance. Of course, we cannot account for the fact that the captive monkeys experienced a barrier between them and the unknown human as he was standing outside the enclosure mesh, however given that the more habituated-wild monkeys also approached to same distance suggest that habituation to humans and/or human artefacts reduces approach neophobia. In contrast to the captive monkeys, the wild monkeys at IVP are exposed to both negative and positive human interactions. Besides researchers (which are distinguished by their blue caps) who sporadically provide food through field experiments, they occasionally encounter poachers, hunters, and people living in villages just outside the reserve fence. Accordingly, the wild-habituated monkeys in our sample have become accustomed to humans and human artefacts but also experience the hazards of natural environments. It is possible that during the experiments, the wild-habituated monkeys perceived researcher presence as a safety indicator, or associated us with occasional feeding opportunities, which possibly raised their motivation to approach the novel stimuli compared to the unhabituated group. Yet, within the sample of habituated-wild monkeys, habituation index did not predict the number of approaches (SI: Table 4S and Fig. 2S), but groups with higher habituation indices had stronger exploration tendencies (Fig. 2). It is also worth emphasising that the majority of the habituated IVP monkeys avoid very close proximity even to familiar humans (Erica van de Waal, personal observation). These findings imply that a significant effect of habituation is the increased motivation to interact and manipulate novel stimuli, rather than just daring to come closer to humans or their artefacts, or expecting to obtain food from them. All together, these findings support our hypothesis that habituation to humans and/or their artefacts facilitates curiosity towards novelty in vervet monkeys.

Going beyond this, within the wild-habituated groups, we found lower explorative tendencies in Lemon Tree and Kubu compared to Baie Dankie and Noha. Indeed, the human-related experiences vary between the habituated groups. The home range of Lemon Tree is located furthest away from the IVP station; and in the previous years, both Lemon Tree and Kubu have encountered hunters/villagers more frequently than other groups. During the habituation process of the monkeys at IVP, Lemon Tree showed a delay in their habituation compared to the other habituated groups (Erica van de Waal, personal communication). Thus, it is plausible that the effect of human habituation on novelty responses is relative to the ratio of neutral-positive (researcher) encounters to neutral-negative (non-researchers, poachers, and hunters) encounters experienced by a group. Furthermore, both Lemon Tree and Kubu have participated in fewer field experiments, and thereby experienced less exposure to manufactured materials and food rewards. Moreover, we found that the groups with the higher habituation indices (Poena, Boata, Noha, and Baie Dankie) explored the plastic cars and rubber butterflies more than the two groups with lower habituation index (Kubu, Lemon Tree) (SI: Fig. 3S). Although these groups have more experiences with colourful items and anthropogenic materials, they also explored seashells more than the other groups, an item that was novel but represents a completely natural material (SI: Fig. 3S). These observations suggest that it was not the material per se that captured their interest but rather that habituation brings about a general change in their curiosity towards unfamiliar items, showing strong support for our habituation hypothesis.

Stimuli type and curiosity

The different stimuli types that we presented to the monkeys did not influence the number of close approaches observed across groups, implying that since all items were new to the monkeys of all groups, each individual needed to approach first to judge whether or not to engage in further exploration.

The categorization of man-made/processed versus more naturalistic stimuli did not have any general effect on responses (SI: Fig. 3S and Fig. 2S). Instead, the data suggest that items that emit a characteristic odour (fish, meatballs, cat toy mice, and boiled pasta) might be less explored on average than non-smelly items. Furthermore, both captive and wild vervet monkeys seemed reluctant to taste the strong-smelling food items fish and meatballs. Former experiments introducing novel foods have demonstrated that it indeed takes vervet monkeys multiple exposures to novel food before they accept it as a food source (Canteloup et al. 2020, 2021) and sociality plays a role in that monkeys are more likely to eat novel food after first observing a conspecific do so (Pooja et al. in prep). Thus, it is likely that monkeys perceive an unknown smell as repulsive and therefore explored such items less. One could argue that popcorn emits similar levels of odour as boiled pasta, yet popcorn was explored much more by the monkeys, especially by the two groups Baie Dankie and Noha (SI: Fig. 3S). These groups regularly participate in field experiments rewarded with soaked corn, and thus, it is possible that the monkeys of Baie Dankie and Noha associated the smell of popcorn with soaked corn, and thereby had a more positive association with the smell of popcorn compared to the other odours. Future experiments should investigate further the effect that odour cues have on novelty responses and exploration tendencies.

Habitat structure and novelty responses

Compared to the wild-habituated groups, it is worth noting that the experiments with the unhabituated wild group always took place underneath a familiar, frequently used sleeping tree, where the monkeys are presumably relatively safe from aerial predators, and with no high grass to obscure potentially hidden snakes, yet this did not seem to increase their motivation to approach (Fif.1). Furthermore, even though open savannah exposes vervet monkeys to large birds and areas of tall grass can hide predatory snakes (Seyfarth et al. 1980), habitat structure had no influence on the motivation to approach novelty during our experiments (Fig. 3a). Previous findings suggest that vervet monkeys at IVP vocalize to recruit social partners, especially close to the river (Mercier et al. 2017), proposing that monkeys experience the river bank as a high-risk area. Thus, distance to the river could potentially be a more relevant variable to assess the influence of habitat on novelty responses. In our sample, habitat structure had no effect on whether or not a monkey approached alone or in a social context (Fig. 3b). This finding was somewhat unexpected, given that sociality has been reported to reduce the risk involved in approaching something new (Stöwe et al. 2006; Moretti et al. 2015), and watching a conspecific interact with novelty also increases exploration tendencies (Forss et al. 2017). Of course, social influences may also constrain an animal's motivation to interact with novel stimuli due to monopolization or potential fear of aggression from conspecifics.

Study limitations

Our study was limited by the inclusion of a single unhabituated group (Congo). Clearly, multiple groups of this category would be needed to verify the effect of habituation across wild monkeys. Moreover, the fact that the Lemon Tree group showed as equally low habituation index as the Kubu group despite the fact that monkeys in Lemon Tree have been regularly exposed to researchers for 3 years more than Kubu raises the question of to what extent within group dynamics potentially influence the monkey's response to novelty. Kubu is a small group with a large proportion of juveniles and in many species, vervet monkeys included, juveniles seem to be more explorative than adults (Fairbanks and McGuire 1993; Bergman and Kitchen 2009; Thornton and Samson 2012; Debeffe et al. 2013). Considering within group dynamics, it will also help to evaluate what effects life-history and sociality have on curiosity. Thus, in the future, we intend to investigate these data at the individual level to clarify how potential within group variation may also contribute to the observed pattern between groups.

Conclusion

One way to detect curiosity in animals is to introduce something novel into their familiar environment and measure their motivation to overcome potential neophobia and explore it. In doing so, we found evidence that curiosity in vervet monkeys is expressed through a combination of reduced neophobia (willingness to approach into close proximity) together with a variety of explorative behaviours like smelling, touching, and tasting something previously unknown (Table 2). Our findings, that captive and wild-habituated vervet monkeys responded more positively towards unfamiliar items than unhabituated conspecifics, despite the fact that all wild monkeys are exposed to similar risks in their natural habitat, support our conclusion that the main driver of curiosity in our sample was habituation level to humans and human-made artefacts, rather than risk constraints or time constraints of life in the wild. Consequently, our findings highlight the importance to account for the captivity effect and habituation levels when conducting cognitive research across settings.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-021-01589-y.

Acknowledgements We are extremely thankful to the research manager Michael Henshall at the IVP and all the volunteers that contributed and assisted our data collection. We are grateful to the van der Walt's family for permission to conduct the study in their reserve. We also dedicate a special thanks to Sandi Cronk at W. A. T. C. H. vervet rehabilitation centre, for her hospitality and collaboration during our stay at the sanctuary. Finally, we thank the Wenner-Gren Foundation, USA and the Waldemar von Frenckell Foundation, Fin to SF and the Swiss National Science Foundation (PP00P3_170624) to EvdW for their financial support for this study. We also would like to thank our reviewers and editor for their feedback that helped improve the manuscript.

Author contributions SF: conceptualization of the study, acquired funding, designing experiments, collected the data, and main writer of the manuscript. AM-R: statistical analyses, text editing, and manuscript writing. PD: assistance by data collection and text editing. TM: assistance by data collection. EvdW: supervisor, provided resources and funding for the study to take place at the IVP, and manuscript editing.

Funding Open access funding provided by Swiss Federal Institute of Technology Zurich. SF: the Wenner-Gren Foundation, USA and the Waldemar von Frenckell Foundation, Finland. EvdW: the Swiss National Science Foundation (PP00P3_170624), Switzerland.

Data availability All data for these analyses can be found in the Open Science Framework with the link: https://osf.io/2cahn/?view_only=e1d66702bc544363b5ced2ae51d97af5.

Code availability The code employed in these analyses can be found in the Open Science Framework with the link: https://osf.io/2cahn/?view_only=e1d66702bc544363b5ced2ae51d97af5.

Declarations

Conflict of interest The authors declare no conflict of interests.

Ethical approval We declare that all experiments performed for this study were conducted on sole observational basis. This research adhered to the "Guidelines for the use of animals in research" of Association for Study of Animal Behaviour and was approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Amici F, Caicoya AL, Majolo B, Widdig A (2020) Innovation in wild Barbary macaques (*Macaca sylvanus*). Sci Rep 10(1):1–2. https://doi.org/10.1038/s41598-020-61558-2

Baayen RH, Davidson DJ, Bates DM (2008) Mixed-effects modeling with crossed random effects for subjects and items. J Mem Lang 59(4):390–412. https://doi.org/10.1016/j.jml.2007.12.005

Barnett SA (1958) Experiments on 'neophobia' in wild and laboratory rats. Br J Psychol 49(3):195–201. https://doi.org/10.1111/j.2044-8295.1958.tb00657.x

Barrett LP, Stanton LA, Benson-Amram S (2019) The cognition of 'nuisance' species. Anim Behav 147:167–177. https://doi.org/10.1016/j.anbehav.2018.05.005

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R Packag Version 1:1–7

Benson-Amram S, Holekamp KE (2012) Innovative problem solving by wild spotted hyenas. Proc R Soc B Biol Sci 279(1744):4087–4095. https://doi.org/10.1098/rspb.2012.1450

Benson-Amram S, Weldele ML, Holekamp KE (2013) A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta Crocuta*. Anim Behav 85(2):349–356. https://doi.org/10.1016/j.anbehav.2012.11.003

Bergman TJ, Kitchen DM (2009) Comparing responses to novel objects in wild baboons (Papio ursinus) and geladas (*Theropithecus gelada*). Anim Cogn 12(1):63. https://doi.org/10.1007/s10071-008-0171-2

Berlyne DE (1950) Novelty and curiosity as determinants of exploratory behaviour. Br J Psychol 41(1):68

Biondi LM, Bó MS, Vassallo AI (2010) Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). Anim Cogn 13(5):701–710. https://doi.org/10.1007/s10071-010-0319-8

Brown GE, Ferrari MC, Elvidge CK, Ramnarine I, Chivers DP (2013) Phenotypically plastic neophobia: a response to variable predation risk. Proc R Soc B Biol Sci 280(1756):20122712. https://doi.org/10.1098/rspb.2012.2712

Byrne RW (2013) Animal curiosity. Curr Biol 23(11):R469–R470

Canteloup C, Hoppitt W, van de Waal E (2020) Wild primates copy higher-ranked individuals in a social transmission experiment. Nat Commun 11(1):1. https://doi.org/10.1038/s41467-019-1420

Canteloup C, Cera MB, Barrett BJ, van de Waal E (2021) Processing of novel food reveal payoff and rank-biased social learning in a wild primate. Sci Rep 11:1–13. https://doi.org/10.1038/s41598-021-88857-6

Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G (2012) How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. Anim Behav 84(3):603–609. https://doi.org/10.1016/j.anbehav.2012.06.015

Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez B (2013) Problem-solving performance is correlated with reproductive success in a wild bird population. Anim Behav 85(1):19–26. https://doi.org/10.1016/j.anbehav.2012.10.005

Damerius LA, Graber SM, Willems EP, van Schaik CP (2017a) Curiosity boosts orang-utan problem-solving ability. Anim Behav 134:57–70. https://doi.org/10.1016/j.anbehav.2017.10.005

Damerius LA, Forss SI, Kosonen ZK, Willems EP, Burkart JM, Call J, Galdikas BM, Liebal K, Haun DB, Van Schaik CP (2017b) Orientation toward humans predicts cognitive performance in orang-utans. Sci Rep 7(1):1–2. https://doi.org/10.1038/srep40052

Day RL, Coe RL, Kendal JR, Laland KN (2003) Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. Anim Behav 65(3):559–571. https://doi.org/10.1006/anbe.2003.2074

Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Coulon A, Gaillard JM, Bon R, Hewison AJ (2013) Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. Anim Behav 86(1):143–151. https://doi.org/10.1016/j.anbehav.2013.05.005

Dobson AJ (2002) An introduction to generalized linear models. Chapman Hall/CRC, Boca Raton

Fairbanks LA, McGuire MT (1993) Maternal protectiveness and response to the unfamiliar in vervet monkeys. Am J Primatol 30(2):119–129. https://doi.org/10.1002/ajp.1350300204

Forss SI, Schuppli C, Haiden D, Zweifel N, van Schaik CP (2015) Contrasting responses to novelty by wild and captive orangutans. Am J Primatol 77(10):1109–1121. https://doi.org/10.1002/ajp.22445

Forss SI, Koski SE, van Schaik CP (2017) Explaining the paradox of neophobic explorers: the social information hypothesis. Int J Primatol 38(5):799–822. https://doi.org/10.1007/s10764-017-9984-7

Forstmeier W, Schielzeth H (2011) Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav Ecol Sociobiol 65(1):47–55. https://doi.org/10.1007/s00265-010-1038-5

Fox RA, Millam JR (2007) Novelty and individual differences influence neophobia in orange-winged Amazon parrots (*Amazona amazonica*). Appl Anim Behav Sci 104(1–2):107–115. https://doi.org/10.1016/j.applanim.2006.04.033

Gajdon GK, Fijn N, Huber L (2004) Testing social learning in a wild mountain parrot, the kea (Nestor notabilis). Anim Learn Behav 32(1):62–71

Greenberg RS (1990a) Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. Anim Behav 39(2):375–379. https://doi.org/10.1016/S0003-3472(05)80884-X

Greenberg RS (1990b) Ecological plasticity, neophobia, and resource use in birds. Studies in Avian Biology

Greenberg RS (2003) The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Reader SM, Laland KN (eds) Animal innovation. Oxford University Press, pp 175–196

Greenberg R, Mettke-Hofmann C (2001) Ecological aspects of neophobia and neophilia in birds. Current ornithology. Springer, Boston, pp 119–178

Greggor AL, Thornton A, Clayton NS (2015) Neophobia is not only avoidance: improving neophobia tests by combining cognition and ecology. Curr Opin Behav Sci 6:82–89. https://doi.org/10.1016/j.cobeha.2015.10.007

Greggor AL, Jolles JW, Thornton A, Clayton NS (2016a) Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position. Anim Behav 121:11–20. https://doi.org/10.1016/j.anbehav.2016.08.010

Greggor AL, Clayton NS, Fulford AJ, Thornton A (2016b) Street smart: faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds. Anim Behav 117:123–133. https://doi.org/10.1016/j.anbehav.2016.03.029

Griffin AS, Tebbich S, Bugnyar T (2017) Animal cognition in a human-dominated world. Anim Cogn 20:1–6. https://doi.org/10.1007/s10071-016-1051-9

Gross ME, Zedelius CM, Schooler JW (2020) Cultivating an understanding of curiosity as a seed for creativity. Curr Opin Behav Sci 35:77–82. https://doi.org/10.1016/j.cobeha.2020.07.015

Gruber T, Clay Z, Zuberbühler K (2010) A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. Anim Behav 80(6):1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Hall BA, Melfi V, Burns A, McGill DM, Doyle RE (2018) Curious creatures: a multi-taxa investigation of responses to novelty in a zoo environment. PeerJ 6:e4454. https://doi.org/10.7717/peerj.4454

Haslam M (2013) 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. Philos Trans R Soc B Biol Sci 368(1630):20120421. https://doi.org/10.1098/rstb.2012.0421

Jarjour C, Evans JC, Routh M, Morand-Ferron J (2020) Does city life reduce neophobia? A study on wild black-capped chickadees. Behav Ecol 31(1):123–131. https://doi.org/10.1093/beheco/arz167

Kalan AK, Hohmann G, Arandjelovic M, Boesch C, McCarthy MS, Agbor A, Angedakin S, Bailey E, Balongelwa CW, Bessone M, Bocksberger G (2019) Novelty response of wild African apes to camera traps. Curr Biol 29(7):1211–1217. https://doi.org/10.1016/j.cub.2019.02.024

Kaulfuß P, Mills DS (2008) Neophilia in domestic dogs (*Canis familiaris*) and its implication for studies of dog cognition. Anim Cogn 11(3):553–556. https://doi.org/10.1007/s10071-007-0128-x

Kidd C, Hayden BY (2015) The psychology and neuroscience of curiosity. Neuron 88(3):449–460. https://doi.org/10.1016/j.neuron.2015.09.010

Kummer H, Goodall J (1985) Conditions of innovative behaviour in primates. Philos Trans R Soc Lond B Biol Sci 308(1135):203–214. https://doi.org/10.1098/rstb.1985.0020

Laidre ME (2008a) Do captive mandrills invent new gestures? Anim Cogn 11(2):179–187. https://doi.org/10.1007/s10071-007-0121-4

Laidre ME (2008b) Spontaneous performance of wild baboons on three novel food-access puzzles. Anim Cogn 11(2):223–230. https://doi.org/10.1007/s10071-007-0104-5

Laland KN, Reader SM (1999) Foraging innovation in the guppy. Anim Behav 57(2):331–340. https://doi.org/10.1006/anbe.1998.0967

Loewenstein G (1994) The psychology of curiosity: a review and reinterpretation. Psychol Bull 116(1):75. https://psycnet.apa.org/. Doi: https://doi.org/10.1037/0033-2909.116.1.75

Martina C, Cowlishaw G, Carter AJ (2021) Individual differences in task participation in wild chacma baboons. Anim Behav 172:73–91. https://doi.org/10.1016/j.anbehav.2020.11.020

McCune KB, Jablonski P, Lee SI, Ha RR (2019) Captive jays exhibit reduced problem-solving performance compared to wild conspecifics. R Soc Open Sci 6(1):181311. https://doi.org/10.1098/rsos.181311

Mercier S, Neumann C, van de Waal E, Chollet E, de Bellefon JM, Zuberbühler K (2017) Vervet monkeys greet adult males during high-risk situations. Anim Behav 132:229–245. https://doi.org/10.1016/j.anbehav.2017.07.021

Mettke-Hofmann C (2014) Cognitive ecology: ecological factors, lifestyles, and cognition. Wiley Interdiscip Rev Cogn Sci 5(3):345–360. https://doi.org/10.1002/wcs.1289

Mettke-Hofmann C, Winkler H, Leisler B (2002) The significance of ecological factors for exploration andneophobia in parrots. Ethology 108(3):249–272

Misslin R, Cigrang M (1986) Does neophobia necessarily imply fear or anxiety? Behav Proc 12(1):45–50. https://doi.org/10.1016/0376-6357(86)90069-0

Morand-Ferron J, Cole EF, Rawles JE, Quinn JL (2011) Who are the innovators? A field experiment with 2 passerine species. Behav Ecol 22(6):1241–1248. https://doi.org/10.1093/beheco/arr120

Moretti L, Hentrup M, Kotrschal K, Range F (2015) The influence of relationships on neophobia and exploration in wolves and dogs. Anim Behav 107:159–173. https://doi.org/10.1016/j.anbehav.2015.06.008

Overington SE, Cauchard L, Côté KA, Lefebvre L (2011) Innovative foraging behaviour in birds: what characterizes an innovator? Behav Proc 87(3):274–285. https://doi.org/10.1016/j.beproc.2011.06.002

Rasolofoniaina BN, Kappeler PM, Fichtel C (2021) Neophobia and social facilitation in narrow-striped mongooses. Anim Cogn 24(1):165–175. https://doi.org/10.1007/s10071-020-01429-5

Reader SM, Laland KN (2001) Primate innovation: sex, age and social rank differences. Int J Primatol 22(5):787–805

Rössler T, Mioduszewska B, O'Hara M, Huber L, Prawiradilaga DM, Auersperg AM (2020) Using an innovation arena to compare wild-caught and laboratory Goffin's cockatoos. Sci Rep 10(1):1–2. https://doi.org/10.1038/s41598-020-65223-6

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1(2):103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Seyfarth RM, Cheney DL, Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210(4471):801–803. https://doi.org/10.1126/science.7433999

Shaw RC, Boogert NJ, Clayton NS, Burns KC (2015) Wild psychometrics: evidence for 'general'cognitive performance in wild New Zealand robins, *Petroica longipes*. Anim Behav 109:101–111. https://doi.org/10.1016/j.anbehav.2015.08.001

Shumaker RW, Walkup KR, Beck BB (2011) Animal tool behavior: the use and manufacture of tools by animals. JHU Press, Baltimore

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

Stöwe M, Bugnyar T, Loretto MC, Schloegl C, Range F, Kotrschal K (2006) Novel object exploration in ravens (*Corvus corax*): effects of social relationships. Behav Proc 73(1):68–75. https://doi.org/10.1016/j.beproc.2006.03.015

R Core Team (2020) "R: 2019." A language and environment for statistical computing version 3.1

Thatcher HR, Downs CT, Koyama NF (2019) Anthropogenic influences on the time budgets of urban vervet monkeys. Landsc Urban Plan 181:38–44. https://doi.org/10.1016/j.landurbplan.2018.09.014

Thornton A, Samson J (2012) Innovative problem solving in wild meerkats. Anim Behav 83(6):1459–1468. https://doi.org/10.1016/j.anbehav.2012.03.018

Tryjanowski P, Møller AP, Morelli F, Biaduń W, Brauze T, Ciach M, Czechowski P, Czyż S, Dulisz B, Goławski A, Hetmański T (2016) Urbanization affects neophilia and risk-taking at bird-feeders. Sci Rep 6(1):1–7. https://doi.org/10.1038/srep28575

van de Waal E, Bshary R (2011) Social-learning abilities of wild vervet monkeys in a two-step task artificial fruit experiment. Anim Behav 81(2):433–438. https://doi.org/10.1016/j.anbehav.2010.11.013

van de Waal E, Borgeaud C, Whiten A (2013) Potent social learning and conformity shape a wild primate's foraging decisions. Science 340(6131):483–485

van de Waal E, van Schaik CP, Whiten A (2017) Resilience of experimentally seeded dietary traditions in wild vervets: evidence from group fissions. Am J Primatol 79(10):e22687

van Horik JO, Langley EJ, Whiteside MA, Madden JR (2017) Differential participation in cognitive tests is driven by personality, sex, body condition and experience. Behav Proc 134:22–30. https://doi.org/10.1016/j.beproc.2016.07.001

van Schaik CP, Burkart J, Damerius L, Forss SI, Koops K, Van Noordwijk MA, Schuppli C (2016) The reluctant innovator: orangutans and the phylogeny of creativity. Philos Trans R Soc B Biol Sci 371(1690):20150183. https://doi.org/10.1098/rstb.2015.0183

Veasey JS, Waran NK, Young RJ (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. Anim Welf Potters BAR 5:13–24

Wang MZ, Hayden BY (2019) Monkeys are curious about counterfactual outcomes. Cognition 189:1–10

Wimberger K, Downs CT (2010) Annual intake trends of a large urban animal rehabilitation centre in South Africa: a case study. Anim Welf 19(4):501

Yamanashi Y, Hayashi M (2011) Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. Am J Primatol 73(12):1231–1238. https://doi.org/10.1002/ajp.20995

Animal Cognition
https://doi.org/10.1007/s10071-023-01765-2

SHORT COMMUNICATION

Juvenile vervet monkeys rely on others when responding to danger

Tecla Mohr[1,2] · Erica van de Waal[2,3,5] · Klaus Zuberbühler[1,2,4] · Stéphanie Mercier[1,2]

Received: 19 October 2022 / Revised: 21 February 2023 / Accepted: 8 March 2023

Abstract
Primate alarm calls are mainly hardwired but individuals need to adapt their calling behaviours according to the situation. Such learning necessitates recognising locally relevant dangers and may take place via their own experience or by observing others. To investigate monkeys alarm calling behaviour, we carried out a field experiment in which we exposed juvenile vervet monkeys to unfamiliar raptor models in the presence of audiences that differed in experience and reliability. We used audience age as a proxy for experience and relatedness as a proxy for reliability, while quantifying audience reactions to the models. We found a negative correlation between alarm call production and callers' age. Adults never alarm called, compared to juveniles. We found no overall effect of audience composition and size, with juveniles calling more when with siblings than mothers or unrelated individuals. Finally, concerning audience reactions to the models, we observed juveniles remained silent with vigilant mothers and only alarm called with ignoring mothers, whereas we observed the opposite for siblings: juveniles remained silent with ignoring siblings and called with vigilant siblings. Despite the small sample size, juvenile vervet monkeys, confronted with unfamiliar and potentially dangerous raptors, seem to rely on others to decide whether to alarm call, demonstrating that the choice of the model may play an important key role in the ontogeny of primate alarm call behaviour.

Keywords Alarm call · Chlorocebus pygerythrus · Audience effect

Introduction

How do animals learn to communicate? One influential model stem from research on vervet monkey alarm calls. Adult monkeys were more selective in their alarm call production than juveniles, who responded to a broader range of species, including many non-predators. Presumably, this was the result of a pruning mechanism by which juveniles learned to ignore irrelevant species (Seyfarth and Cheney 1980). Social learning plays a key role (León et al. 2022) but how exactly infants and juveniles obtain the relevant information from others is largely unknown. One key step in successful social learning when learning alarm call is to select appropriate models, i.e., individuals that are competent and reliable. Age and genetic relatedness are likely to be relevant to the choice of the model and there is evidence in meerkats that caller reliability is a relevant feature (Rauber and Manser 2018). Similarly, infant vervet monkeys are more likely to react appropriately to alarm call if they first look at an adult's reaction compared to others less reliable individuals (Seyfarth and Cheney 1986).

In this study, we were interested in how juvenile vervet monkeys assess their audience during alarm call events. This species is interesting, because adults possess acoustically distinct alarm calls to raptors, terrestrial carnivores and dangerous snakes (Seyfarth et al. 1980), a capacity that develops gradually during ontogeny, as outlined before (Cheney and Seyfarth 1980). To investigate this behaviour process of giving the correct alarm call according to the

---

Klaus Zuberbühler and Stéphanie Mercier are joint senior authors.

✉ Tecla Mohr
mohr.tecla@gmail.com

[1] Comparative Cognition Laboratory, University of Neuchâtel, Neuchâtel, Switzerland

[2] Inkawu Vervet Project, Mawana Game Reserve, Swart Mfolozi in Kwazulu-Natal, South Africa

[3] Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

[4] School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland, UK

[5] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, P/Bag X01, Durban 3209, South Africa

predator, we presented small unfamiliar raptor models (Fig. S1) to juvenile vervet monkeys (1–2 years old) surrounded by audiences of different compositions, which can be used as a reliable indicator of danger, knowing whether or not to alarm call. For age, we predict that adults will categorise the models as harmless (due to their knowledge and experience) and therefore will not alarm call, while we will expect juveniles to categorise the models as potentially dangerous (due to their resemblance with familiar raptors), and, therefore, to produce alarm calls. Consequently, we will predict juveniles to alarm call in presence of their siblings and their mother but they will remain silent in presence of unrelated conspecifics. Regarding audience size and behaviour, we will predict juveniles to alarm call less in larger than smaller subgroups (due to the likelihood of being surrounded by at least one older group member) and to adapt their alarm call whether mothers and siblings are vigilant assuming that kin would be more trustworthy than non-kin to warn them about danger.

Methods

The study was conducted over a period of 6 months (30 September 2016–19 March 2017) on three groups of wild vervet monkeys (BD, KB and NH) at the Inkawu Vervet Project (IVP) in Mawana Game Reserve, South Africa (Table S1). Subjects were 15 juveniles ($N=9$ males; $N=6$ females; Table S2). We presented unfamiliar raptor models to 15 subjects under three different social conditions (mother, siblings, or unrelated group members), leading to 45 counterbalanced trials. In mother's condition, we waited until the subject's mother was within 10 m, making sure that no siblings were present. In the siblings' condition, we waited until the subject had at least one of his/her siblings present within 10 m, making sure that the mother was absent from the audience. In the unrelated group members 'condition, we waited until the subject had at least one unrelated conspecific within 10 m, making sure that his/her mother and all siblings were absent. We recorded the reaction as soon as the subject looked in the direction of the model and modified its behaviour (model considered as being detected), which was usually accompanied by vigilance (stopping previous activity and gazing towards model) and/or producing alarm call. Observations finished as soon as the model was covered under a textile. We defined any individual within a 10 m radius of the subject as part of the subject's audience, which we identified individually and monitored as much as possible in terms of their behaviours. We defined vocal trials as all trials in which at least one alarm call bout had been produced, either by subjects or by other participants.

For each experiment, we collected data on, social condition (mother, siblings, unrelated group members), raptor model (two different ones were used to avoid habituation), subject identity, subject behavioural responses, audience composition (identities of all individuals within 10 m of subject), as well as mother and siblings' behaviour (ignored, vigilant, alarm called) in our models. For our analysis, we excluded two experiments from the 45 trials, because another individual than the subject had already produced at least one alarm call and could have thus influenced its response. We further removed three trials where the audience reaction was not visible, leading to a total of 40 trials analysed (Table S3). Unfortunately, sample sizes were too small to conduct any statistically meaningful analysis for caller's age, audience size, age, or reaction. Instead, we present here a descriptive analysis of the main finding. We used generalised linear mixed models (GLMM; Baayen et al. 2008), fitted with a binomial structure and logit-link function with Laplace approximation, to investigate whether juveniles adapted their vocal behaviour according to audience composition (see Supplements: Additional information). Data were analysed with R Studio 3.2.1 (Team 2015). For the GLMM, we used the packages 'arm' (Gelman 2016), 'car' (Weisberg 2011), 'faraway' (Faraway 2016), and lmerTest (Kuznetsova et al. 2017).

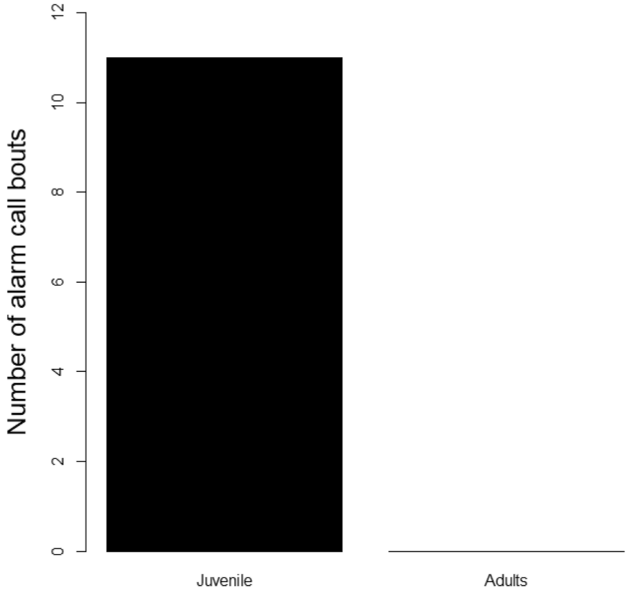


Fig. 1 Number of alarm call bouts produced by juveniles and adults

Results

$N = 69$ individuals participated in $N = 40$ trials, but only $N = 9$ juveniles alarm called (13.0%, $N = 11$ alarm call bouts total, Fig. 1); with two individuals alarm calling in more than one trial (Table S4). Overall, we found that audience composition did not influence the alarm calling behaviour of juveniles (GLMM, Table S5). However, we observed subjects remaining silent in the presence of their mothers (10 of 11 trials), and to a lesser extent, in the presence of unrelated conspecifics (12 of 15 trials), which was not the case in the presence of siblings (6 of 14 trials; Fig. 2).

We were unable to systematically control for audience size, which ranged from 1 to 11 individuals (Fig. 3).

Regarding the audience reaction, it appeared that whether or not the mother was vigilant may have guided whether the juvenile called (Fig. 4, panel a), whereas the vigilance of siblings did not appear to guide juveniles alarm calling (Fig. 4, panel b).

Discussion

In this study, we were interested in how juvenile vervet monkeys adapted their anti-predator behaviours when encountering raptor models according to their social environment. First, we found a correlation between caller's age and alarm call production (Fig. 1), decreasing the production of alarms with age. While adults never alarm called to the models, younger vervet monkeys were more

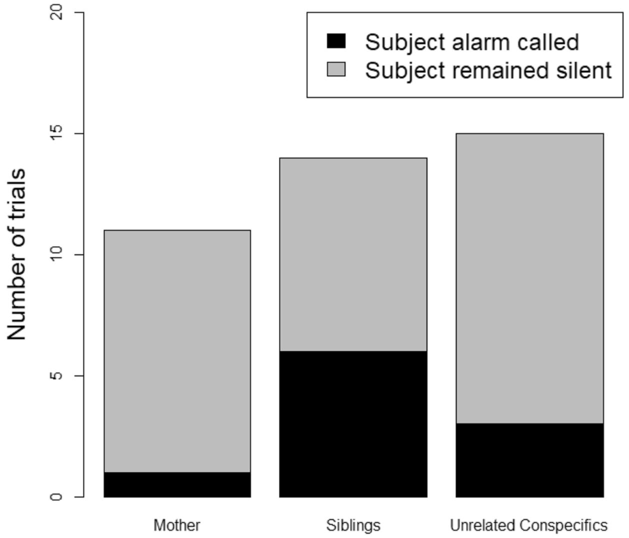


Fig. 2 Number of trials in which subjects alarm called (black) or remained silent (grey) in presence of mother, siblings and unrelated conspecifics

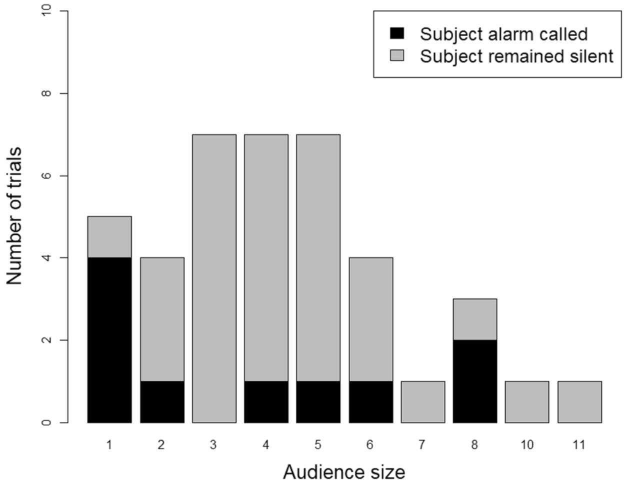


Fig. 3 Number of trials in which subjects alarm called (black) and remain silent (grey) in presence of audience size composed of group members from 1 to 11 individuals

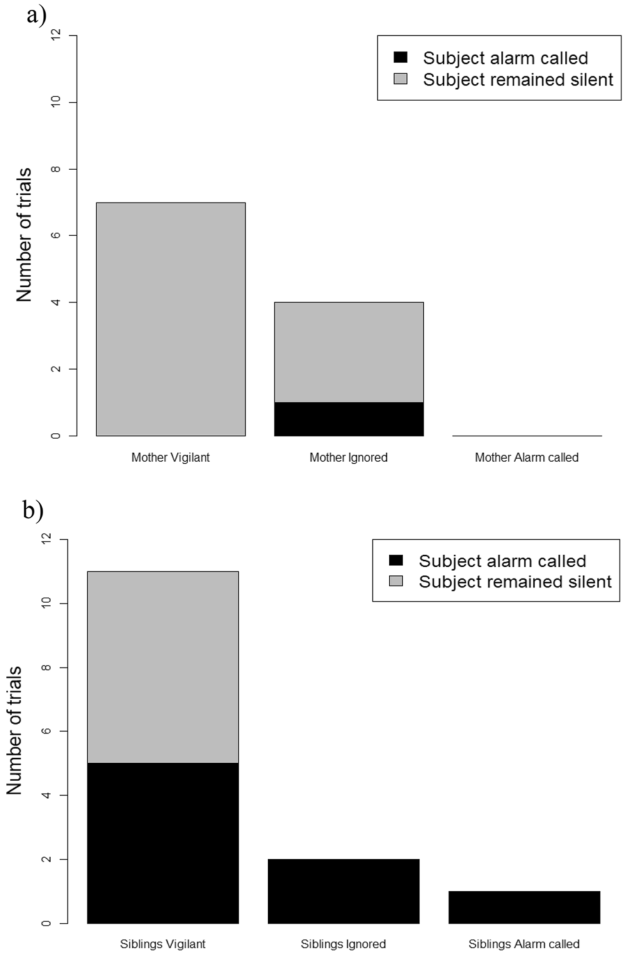


Fig. 4 Number of trials in which subjects alarm called (black) and remained silent (grey) in presence of mother (**a**) and siblings (**b**) showing three different reactions to the predator model: vigilant, ignored, alarm called

likely to alarm call. This is likely explained by the fact that inexperienced juveniles often alarm called to a wider range of animals, including harmless ones (Seyfarth and Cheney 1980; Wegdell et al. 2019; Wich and de Vries 2006), whereas adults produce alarm calls to specific dangerous known predators.

In a second step, we observed that juveniles were more likely to remain silent in presence of mothers, and to a lesser extent, in presence of unrelated group members, while they were more likely to alarm call in presence of siblings (Fig. 2). Social learning from more experienced individuals could be a potential interesting explanation of why juveniles alarm called less in presence of their mother. Young individuals might benefit from observing the reaction of experienced models to develop more adapted anti-predatory responses.

Finally, regarding audience behaviour, we observed that mother's vigilance appeared to guide infant alarm calling, but siblings' vigilance status did not. Subjects alarm called more when the mothers ignored the model, while they remained silent when their mothers were vigilant. This might be explained by a level of awareness since vigilant mothers were clearly aware of the harmless models, while ignoring ones might not be aware of a potential danger nearby. However, we found that juveniles were alarm calling more in presence of siblings who ignored the models, but we did not see any effect in presence of vigilant siblings. Despite the same explanation should be true for siblings than mothers, here, it is possible that results were confounded by kin selection, as it might always be more valuable to alarm call in presence of kin regardless of their awareness, especially if they are younger and thus more vulnerable than the caller. Unfortunately, all our sample sizes are very low and future studies should be conducted to address all these hypotheses with a decent sample size for proper statistical testing.

Conclusion

In many social animals, alarm calls are essential components of "sometimes-complex" anti-predator strategies, but little is known about how audience and kin selection influence alarm calling behaviours in juveniles. In our project, we found that young vervet monkeys appeared to adjust their alarm calling behaviour depending on the experience in their audience, with increased alarm call production in presence of siblings, compared to when they were with their experienced mothers or unrelated conspecifics. It appears that experience (i.e., age), kinship (mothers and siblings) and specific characteristics of audience (whether or not they are vigilant) all influence the alarm calling of juvenile vervets. Further studies with larger sample sizes are needed to further explore the influences of the social environment in primate vocal development.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-023-01765-2.

Acknowledgements We are grateful to K. van der Walt for permission to conduct the study at Mawana game reserve and to Ezemvelo KZN Wildlife who provided us the permission to conduct our research on wild vervet monkeys in South Africa. We are also grateful to A. van Blerk for managing the Inkawu Vervet Project, and all the team from IVP for their support and help in data collection, with a special thanks to S. Hamilton, C. Morais Pacheco, H. Saint-Jean and A. Couchouron who provided a great help in carrying out the experiments. Finally, we are grateful to J.M Freyermuth, F. Schütz, L.Dib and R. Harrison for their help with the statistical analyses and C. Neumann for interesting discussions.

Author contributions TM participated in the design of the study, collected field data, participated in data analysis and drafted the manuscript; EvdW coordinates the research at IVP in South Africa, helped financially and commented on the manuscript; KZ conceived and participated in the design of the study, financed the study and corrected the manuscript and SM conceived and designed the study, coordinated the study, participated in data analysis and drafted the manuscript. All authors gave final approval for publication.

Funding Open access funding provided by University of Lausanne. Funding was provided by FP7 Ideas: European Research Council, 283871, Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, 310030_143359, PP00P3_170624, Branco Weiss Fellowship-Society in Science.

Declarations

Conflict of interest The authors declare no conflict of interests.

Ethical approval Our study was approved by Ezemvelo KZN Wildlife and the University of Cape Town, South Africa and adhered to the ASAB/ABS guidelines for the use of animals in research (Buchanan et al. 2012). All animals were well habituated to human observers and could be individually identified. Our experimental manipulation was similar to a large number of related field studies, all based on the notion that simulating natural predator encounters is ethically acceptable, provided it is done within the natural range of experiences (Zuberbühler and Wittig 2011). For example, when presenting the models, we respected a timeline that corresponded to a natural rate of predator encounters, as recommended for such types of field experiments (Zuberbühler and Wittig 2011). Encountering potentially dangerous animals is part of most animals' natural lives, suggesting that our model experiments did not impose ethically unacceptable circumstances on our study groups. We recorded no injuries or signs of long-term disturbance during this study. We also noted that, once the predator models were removed from sight, monkeys typically resumed their previous activities very rapidly.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Baayen RH, Davidson DJ, Bates DM (2008) Mixed-effects modeling with crossed random effects for subjects and items. J Mem Lang 59(4):390–412

Buchanan et al. (2012) Guidelines for the treatment of animals in behavioural research and teaching. Animal Behav 83(1):301–309

Cheney DL, Seyfarth RM (1980) Vocal recognition in free-ranging vervet monkeys. Anim Behav 28(2):362–367

Faraway JJ (2016) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. CRC press

Gelman A, Su YS, Yajima M, Hill J, Pittau MG, Kerman J (2016) Data analysis using regression and multilevel/hierarchical models. R package version 1.9–3 p. 1.5–04. Accessed 28 Aug 2022

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: tests in linear mixed effects models. J Stat Softw 82(13):1–26. https://doi.org/10.18637/jss.v082.i13

León J, Thiriau C, Bodin C, Crockford C, Zuberbühler K (2022) Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. Iscience 25(9):104853

Rauber R, Manser M (2018) Experience of the signaller explains the use of social versus personal information in the context of sentinel behaviour in meerkats. Sci Rep 8(1):1–7

Seyfarth RM, Cheney DL (1980) The ontogeny of vervet monkey alarm calling behavior: a preliminary report. Z Tierpsychol 54(1):37–56

Seyfarth RM, Cheney DL (1986) Vocal development in vervet monkeys. Anim Behav 34(6):1640–1658

Seyfarth RM, Cheney DL, Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210(4471):801–803

Team R (2015) RStudio: integrated development for R. https://www.rstudio.com/. Accessed 29 Mar 2023

Wegdell F, Hammerschmidt K, Fischer J (2019) Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. Nat Ecol Evol 3(7):1039–1042

Weisberg JFAS (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks

Wich SA, de Vries H (2006) Male monkeys remember which group members have given alarm calls. Proc R Soc Lond B Biol Sci 273(1587):735–740

Zuberbühler K, Witting RM (2011) Field experiments with non-human primates: a tutorial. In: Field and laboratory methods in primatology: a practical guide. Cambridge Univ.Pr, pp 207–224