Cognitive personality traits in semi-urban Vervet Monkeys

M.Sc. Project

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Abstract

The rapid decline of natural habitats and the increasing development of urban areas poses significant challenges for many species. The extent to which a species is successful in adapting to these environmental changes is suggested to depend on a species general behavioural and cognitive flexibility. Behavioural traits, like reduced neophobia and increased interest in exploring novelty, in other words *"curiosity"* are important mechanisms for innovative adaptation to novelty. Vervet monkeys *(Chlorocebus pygerythrus)* are one of relatively few primate species that have successfully adapted to urban environments, thus making them an ideal species to study behavioural and cognitive flexibility. Here, using a within-species approach, we systematically compared motivational cognitive traits of neophobia and curiosity in semi-urban living populations with wild and captive populations of vervet monkeys to shed light on the underlying psychological mechanisms responsible for their successful urban living. To measure neophobia and curiosity we exposed monkeys to a test battery of various types of novel stimuli and quantified their behavioural responses. Our results revealed no differences in number of approaches to novel stimuli nor the level of exploration between semi-urban and wild monkeys. However, captive monkeys were significantly more explorative than both semi-urban and wild groups, suggesting that positive experiences with humans and lack of predation plays a role in exploratory behaviour rather than exposure to human artefacts per se. Our findings also indicate that juvenile males were more explorative across groups, likely due to males being the dispersal sex and juveniles being more motivated to learn about their environment. Additionally, we found that novelty, potentially associated with human food packaging elicited stronger explorative responses in semi-urban groups, suggesting that their motivation to explore may be driven by previously rewarding foraging on similar anthropogenic food sources. We conclude that varying levels of exposure to humans/human artefacts, predation and pre-exposure to human food packaging may explain variation in curiosity in our sample of vervet monkeys.

Introduction

As spaces for wildlife continues to decline, animals must cope with immense changes or face extinction. One way for animals to cope with such changes is to exploit newly available, or previously unused resources (Greenberg 2003). Many animals have been observed exploiting new resources by adapting new behaviours arising from new innovative ways of accessing food sources, for example the sweet-potato washing of Japanese macaques (*Macaca fuscata)* and the milk-opening behaviour of blue tits (*Cyanistes caeruleus)*. The innovation of new behaviours and rapid learning is important mechanisms for species to successfully adapt to novel resources (Lefebvre et al. 1997, Brooke et al. 1998, Estes et al. 1998, Berger et al. 2001). Innovation is commonly referred to the ability to react with a novel response to a familiar problem, or to produce a novel solution to an existing problem (Kummer and Goodall 1985, Greenberg 2003b). Many foraging behaviours of urban wildlife incorporates ability to innovate (Klump et al. 2021). The Cognitive Buffer Hypothesis (CBH) suggests that species with advanced cognitive abilities should be able to alter their behaviour in response to environmental changes through adaption of novelty through innovation and behavioural flexibility (Sol 2009). Support for the CBH originated in previous research that that showed bird species with higher innovation rates were the most likely to invade novel habitats successfully (Sol et al. 2002, 2005, 2016). Primates are well known for their advanced cognitive abilities and traits (Kummer and Goodall 1985, Reader and Laland 2002, Hopper 2016, Ebel et al. 2019, Bandini and Harrison 2020). We therefore should expect the successful adaptation of primate species to human-altered environments to progress through innovative and flexible behaviour. Yet, we see very few species of non-human primates thriving in the urban world, partly through their high conflict potential with human niche. Further, for those primates that do thrive, we know very little about the extent to which motivation and cognition are involved in their success.

Cognition is the ability to retain and process information and use gained knowledge subsequently. As such, a species underlying motivational traits to gather new information (neophobia and curiosity) will be decisive for adaptation to environmental changes and to innovatively use new resources. Moreover, within a species these motivational traits also define an animal's personality and are typically included in studies on animal personalities (Grunst et al. 2019). Correlations between personality traits are likely maintained through constraining mechanisms that inhibit behavioural changes (i.e., "constraint hypothesis"; Bell

2005) or through certain traits being selected for in some distinct environments (i.e "adaptive hypothesis"; Lande and Arnold 1983, Bell 2005). Certain personality traits, such as exploratory behaviour, are known to exhibit high consistency over time and across different situations. Moreover, personality traits like neophobia and curiosity, are believed to offer advantages for adapting to new environments (Phillips and Suarez 2012). These advantages can be direct, such as facilitating the discovery of novel resources, as well as indirect, by influencing the development of flexible and adaptable behavioural responses (Sol et al. 2011). Variation in neophobia and exploration tendency can be attributed to numerous factors such as level of habituation to humans, age, or environment (Forss et al. 2015, 2022, Johnson-Ulrich et al. 2021). Thus, studying these traits can provide insight into the adaptation of a species to a human-altered ecosystem and a species' pathway to novelty adaptation.

Neophobia is often used to describe the fear of novelty (Greenberg 1990, 2003b, Fox and Millam 2007, Greggor et al. 2016b, 2016c, 2016a). However, due to difficulty in interpreting fear in animals, the term "novelty avoidance" is more often used (Misslin and Cigrang 1986, Benson-Amram et al. 2013, Greggor et al. 2015, Forss et al. 2015, Rasolofoniaina et al. 2021). Individuals that are less bold or less explorative, sometimes also termed neophobic, are less likely to interact with novel stimuli (Réale et al. 2007, Carter et al. 2012). By studying food neophobia, we can determine how individuals perceive new resources and how willing they are to incorporate new foods into their diet, while object neophobia can indicate how well a species can respond to changes within their environment.

While neophobia is a psychological function that likely protects animals from the danger of the unknown (Greenberg 2003a), it can simultaneously prevent an animal from detecting a potentially beneficial resource that may be crucial to species' survival, especially when a species is invading habitats characterized of high rate of changes. Therefore, an essential step towards engaging in curiosity-driven exploration lies in how animals overcome neophobia. For most species both natural and urban environments can be unpredictable and pose high-risk factors such as cars and pets. Accordingly animals need to balance the risks versus benefits and accordingly exhibit appropriate levels of neophobia (Barnett 1958, Greenberg 1990, Mettke-Hofmann et al. 2002). Many researchers are trying to understand the mechanisms that reduce neophobia or influence individual variation in

curiosity-driven exploration (Pliner et al. 1993, Monneuse et al. 2008, 2011, Mettke-Hofmann 2017).

Curiosity, defined as "a motivation to seek out and acquire information about something unfamiliar" (Berlyne 1950, 1960, 1966, Loewenstein 1994, Byrne 2013, Kidd and Hayden 2015, Gross et al. 2020) and is an important underlying mechanism of active learning and creativity in humans and other animals (Burda et al. 2018, Tian et al. 2021). Yet its function and evolutionary roots are poorly understood. In animal studies curiosity is measured through the motivation to gather information about something unfamiliar, outside of the context of survival behaviour (Mettke-Hofmann et al. 2002, Byrne 2013, Hall et al. 2018). Studying these interlinked traits, it is essential to bear in mind that being explorative does not contradict being neophobic. Instead, explorative behaviours encompass various motivated actions aimed at acquiring information about unfamiliar stimuli (Greenberg 2003c, Biondi et al. 2010, Carter et al. 2012, Forss et al. 2015). Thus, an animal can exhibit both neophobia and a strong inclination towards exploration simultaneously (Moretti et al. 2015, Forss et al. 2015). In this context, curiosity refers to a positive response to novel stimuli, manifested through a combination of low neophobia (measured as a willingness to approach something new) and subsequent explorative behaviours employed by an individual to gather knowledge about newly encountered stimuli (measured as exploration events, such as handling, sniffing, etc.) (Damerius et al. 2017b).

Animals in captivity have been known to exhibit extremely reduced levels of neophobia due to the risk-free environment in which captive animals live (Barnett 1958, Brown et al. 2013). This "captivity effect", postulates that within a species cognitive differences exist between captive and wild populations (Haslam 2013, Forss et al. 2015, van Schaik et al. 2016, Rössler et al. 2020), which has been attributed to various not mutually exclusive factors. The "free time hypothesis' and the "excess energy hypothesis" both propose that wild populations tend to be far more occupied with foraging and predator vigilance that captive populations, thus allowing captive populations to have an energy surplus and excess time for exploratory behaviours (Kummer and Goodall 1985, Laidre 2008, Amici et al. 2020). Additionally, the "captivity effect" has been shown to result from habituation to humans and human artefacts in some species (Mountain parrots; Gajdon et al. 2004; Orangutans; Damerius et al. 2017a, 2017b, Forss et al. 2015; Vervet monkeys;

(Waal and Bshary 2011, Forss et al. 2022). Studies on orangutans (Pongo abelii and Pongo pygmaeus) have shown that human presence induces curious responses in highly neophobic wild orangutans and in captive orangutans increased exposure to humans was positively correlated with exploration tendency (Damerius et al. 2017a, 2017b). Therefore, it is likely that the "captivity effect" is due to human habituation in some species resulting in increased interest in novelty and reduced risk perception of humans (Waal and Bshary 2011; Damerius et al. 2017a, Forss et al. 2022).

Ultimately, how animals perceive different novel stimuli depend on their past experiences and thus behavioural responses and the interest in novelty will reflect the balance of perception and experience (Moretti et al. 2015). Urban animals provide great opportunities to gain insights in what drives novelty exploration. Firstly, b urban populations are frequently in contact with human artefacts and are using human food sources in their regular diet, and therefore individuals will associate some objects such as takeaway boxes and trash bags with food and thus will be more motivated to explore them due to potential access to food. Unlike captive populations, urban living animals are often treated as pests or nuisance species, and thus experience the negative side of humans, as opposed to being cared for by them. Additionally, urban populations are exposed to higher levels of risks than captive populations, such as traffic accidents, electric fences, pets, and lack of space.

In this study, we investigated exploratory tendencies in semi-urban, wild, and captive vervet monkeys (Chlorocebus pygerythrus), by using novel-object paradigms. Vervet monkeys present a compelling opportunity to investigate curiosity due to their remarkable adaptability as opportunistic foragers. These primates demonstrate successful adaptation to anthropogenic environments, including agricultural and urban areas, where they often exploit human food sources (Wimberger et al. 2010, Thatcher et al. 2019). Given their classification as a highly adaptable and ubiquitous species, we anticipate vervet monkeys to exhibit relatively low levels of neophobia and pronounced exploratory tendencies towards novel stimuli. As generalists and sometimes regarded as "nuisance" species, their behavioural repertoire is likely characterized by a propensity for curiosity-driven exploration (Greenberg 2003c, Sol et al. 2011, Tryjanowski et al. 2016, Griffin et al. 2017, Barrett et al. 2019, Jarjour et al. 2020). Specifically, we performed an intraspecific comparative investigation of motivational cognitive traits in vervet monkeys living in an urban setting, captivity and in the wild. First, we compared the responses to novel stimuli of semi-urban

monkeys to those of wild and captive monkeys. We predicted that if there is a captivity effect, semi-urban and wild monkeys will show significantly less interest in novelty than captive conspecifics. Additionally, due to higher levels of risks than captive populations and potentially a high level of human habituation semi-urban populations are predicted to balance between captive and wild population in exploratory behaviour (Forss et al. 2021). In addition, we investigated whether the individual effects of age and sex had any influence on the monkey's response to novelty across all groups. Here, our prediction was that juveniles and males would be more motivated to explore novelty due to juveniles needing to a fill a learning need about their environment and males being the dispersal sex (Fairbanks and McGuire 1993, Bergman and Kitchen 2009, Thornton and Samson 2012, Debeffe et al. 2013). Finally given that semi-urban, wild, and captive monkeys differ in the experiences with human-made items, we used objects of natural and artificial characteristics and tailored specific objects to the semi-urban groups to evaluate any potential effects of stimuli. We predicted that due to their already high exposure to novelty, semi-urban groups will be more inclined to explore objects that they perceive to be associated with a food reward.

Methods

Subjects and Study Sites

We collected observational data on semi-urban vervet monkeys through ad libitum data and focal follows between October 2022 and March 2023 and we conducted field experiments on exploration behaviour between January 2023 and March 2023 at the Urban Vervet Project (UVP) field site, located in the Simbithi eco estate in Ballito, KwaZulu-Natal, South Africa. The study site is a private gated community with various housing and leisure areas and is home to multiple free-roaming troops of vervet monkeys. This environment is defined as semi-urban due to a high degree of natural spaces within the eco-estate, in comparison with a city or suburb. The estate encourages wildlife research for better biodiversity management and reducing human-wildlife conflict. Since this was the initial phase of the project, only one habituated troop, the Acacia troop (N=21), was available for experiments at this stage. The troop's previous history was unknown, but most monkeys were well habituated to human presence due to daily exposure. Before the experiments, we spent four months collecting behavioural observations and identifying individual monkeys. A

total of 22 individuals were identifiable based on behaviours, injuries, and facial markings (ID file, supplementary material). The study area which consisted of the northwest corner of Simbithi also contained three other troops, with many more troops residing throughout the rest of the eco-estate.

For comparative reasons we analysed our data on semi-urban vervet monkeys to that from already collected datasets from both wild and captive vervet monkeys. Data on wild vervet monkeys was collected by SF in February and March 2020 at the Inka Vervet Project (IVP) field site, located in the Mawana game reserve in KwaZulu-Natal, South Africa. This field site is home to several habituated vervet monkey troops regularly observed by researchers and participating in experimental studies. The dataset includes four of these troops, three of which have been habituated since 2010 (Baie Dankie: N = 57, Noha: N = 39, Lemon Tree: N = 24), and the fourth since 2013 (Kubu: N = 19). Additionally, the reserve hosts at least three unhabituated troops in the study area, with many more residing throughout the rest of the reserve. Data on captive vervet monkeys was collected in March 2020 by Dr Sofia Forss at the Wild Animal Trauma Centre & Haven (WATCH) vervet sanctuary in Vryheid, KwaZulu-Natal, South Africa. The WATCH sanctuary housed three troops at the time of data collection, but for logistical reasons, only one group were included in this study (Poena: N = 17). Many of the monkeys in this sanctuary have been cared for by humans since they were a few weeks old, with only a few rescued later in life. When infant monkeys arrive, they are initially housed indoors, and bottle nursed. At three months of age, they are gradually integrated into a troop. As the main goal is to release individuals back into their natural habitat, both caretakers and researchers limit their contact with the monkeys as much as possible.

Experimental Setup

Semi-urban monkeys

We presented the Acacia troop with nine stimuli representing various distinct materials, colours, and structures. Six of these items were characterized as distinctly human-made: nailbrushes, baby bottles, trash bags, balls (ping pong and golf), takeaway boxes, and baby teethers. The trash bags, balls, and takeaway boxes represent familiar objects in an urban setting, while nailbrushes, baby bottles, and baby teethers represent potentially novel objects. Two items, snail shells and seashells, represented naturally occurring objects

from a different habitat and were thus assumed novel to this monkey group. The remaining item was man-made but with naturalistic features: plastic colourful butterflies. The presentation of these items was randomized to avoid order effects, and each type of novel stimulus was presented one at a time. We placed exactly twelve copies of each stimulus one meter apart to reduce monopolisation of objects by dominant group members. To attract the attention of the monkeys a handful of soaked corn was placed in the middle of the experimental area. Two weeks before conducting the experiments, we fed the monkeys a small amount of corn to confirm that it was a desirable food source for them. The main goal of the experiments was to record any potential reactions towards the novel stimuli after attracting the monkeys to the area (within 20m). The experiments were conducted at various times throughout the day with most experiments taking place in the early hours of the morning (1-2 hours after sunrise). Only one stimulus was presented each day with a minimum of one day between each experiment. We recorded all experiments with Sony handheld cameras HDR-CX200, with one camera mounted on a tripod and the other being held by an observer zooming in on any explorative behaviours. The experiments were 20 minutes in length, to allow enough time for low-ranking individuals to have opportunities to explore the objects. Both experiments with baby teethers and snail shells were conducted under camera traps to evaluate any potential effects of human presence on explorative behaviours. The camera trap experiments were filmed with two Bushnell 30MP Trophy Cam Dual-Core Treebark Camo Low Glow wildlife camera traps set up 10m apart on opposite trees to record all possible behaviours associated with the objects. All experiments were conducted in familiar and safe areas to the monkeys, napping and sleeping sites with low grass coverage for better viewing of explorative behaviours.

Wild troops

All four habituated groups were presented with eight novel stimuli of different materials, colours, and structures. For the comparative analysis here only three of the stimuli were used with the semi-urban troops: plastic butterflies, and seashells. The same experimental protocol for the semi-urban groups was used: numbers of novel stimuli, experimental duration, and handheld placements.

Captive troops

At the WATCH sanctuary, novel stimuli were placed in the main enclosure of the monkey. The experimental setup was kept the same as both the semi-urban and wild troops to ensure data is comparable. The only difference was the use of peanuts to attract the monkeys as opposed to soaked corn as the captive monkeys were more familiar with peanuts.

Video coding and measurements

All behaviours were identified and coded from video recordings using the video coding software Cowlog. The number of proximity approaches were defined as an approach made to around 1m of any of the objects. The number of approaches were determined by the number of times each monkey made an approach. For each approach towards the objects and experimental area, we also distinguished whether the approach was made socially (when another monkey was present around 1m of an object) or alone (where no monkeys were present near any of the objects). Once a monkey made physical contact with an object (0m), we coded: number of touches, sniffs, tastes, chews, and number of times an object was moved/lifted. We then summed these behaviours into one exploration score and noted the duration of exploration.

Statistical analyses

We conducted the statistical analyses in R (version 4.3.0; R Core Team, 2023) and RStudio (version 2023.03.1+446; RStudio Team, 2023). To address the study aims, we fitted five different model; Generalized Mixed Models (glmm) to the data. We checked all models for overdispersion and overall stability. We draw inference by comparing the full model with a null model that lacks predictors but contains all other model elements (Forstmeier and Schielzeth 2011) using a likelihood ratio 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.

The first models analysed individual curiosity in all groups (Model 1a), we evaluated potential differences in the explorative behaviour among the different group types (3 levels:

captive, wild, and semi-urban), and stimuli type (2 levels: butterflies and seashells). The exploratory behaviour is used by the count variable exploration score which is a total of all exploratory behaviour (touched, moved, licked, sniffed, tasted) for each individual and the number of grid approaches (approaches to novel stimuli). The variable individual was used a random effect to account for random variation between individuals.

In the second model (Model 2a), we investigated the effects of age (four levels: infant, juvenile, and adult), sex and stimuli type (nine levels: see above) on the number of approaches to the novel stimuli (response variable, count data) observed in the semi-urban group. In model 1b we evaluated potential differences in exploration score based on type of stimuli type (9 levels) in the semi-urban group. A negative binomial distribution was used in this model to account for overdispersion. In both models, individual was used as a random effect.

In Model 3, we evaluated the effects of interindividual differences of sex and age (3 levels: infant, juvenile, and adult) on exploratory behaviour (exploration score). We included individual ID and group ID (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) as random effects to account for random variation across groups and individuals.

Table 1: Descriptions of the different model structures. Group size was log-transformed before being introduced as an offset.

Model	Response variable	Fixed effects	Random effects	Offset
1a	Number of approaches	Age + sex + Stimulus	Individual	
1b	Exploration score	Age + sex + Stimulus	Individual	
2a	Number of approaches	Environment + stimulus (interaction)	Individual	Log group size

2b	Exploration score	Environment + stimulus (interaction)	Individual	Log group size
3	Exploration score	Age + sex	Group ID (4 levels) + Individual	

Results

Group level analysis

Model 1a was overall significantly different from the null model (likelihood ratio test: X^2=37.19, df=5, p<0.0005; R^2 full model=0.25.) Group type had a significant effect on monkeys' approach to the novel stimuli (group type: p<0.0001), while stimulus had no effect (stimulus: p=0.1). More specifically we found that captive groups presented the highest average number of close approaches to the novel stimuli (captive-wild: P=0.001, Hedge's g=1.49; captive-urban: p=0.001, Hedge's g=1.70, see fig 1). Model 2b was also significantly different from the null model (likelihood ratio test: X^2=110, df=7, p<0.0001; R^2 full model=0.94). Group type (captive) additionally had a significant effect on the level of exploration of novel stimuli (group type: p<0.0001), while both plastic butterflies and seashells had the same number of explorative events (84) out of all groups with the captive groups accounting for more than half of exploratory events for seashells (53). Overall captive groups had a higher exploration score than both wild and semi-urban groups (captive-wild: P=0.001, Hedge's g=1.27; captive-urban: p=0.001, Hedge's g=1.69, see fig 2).

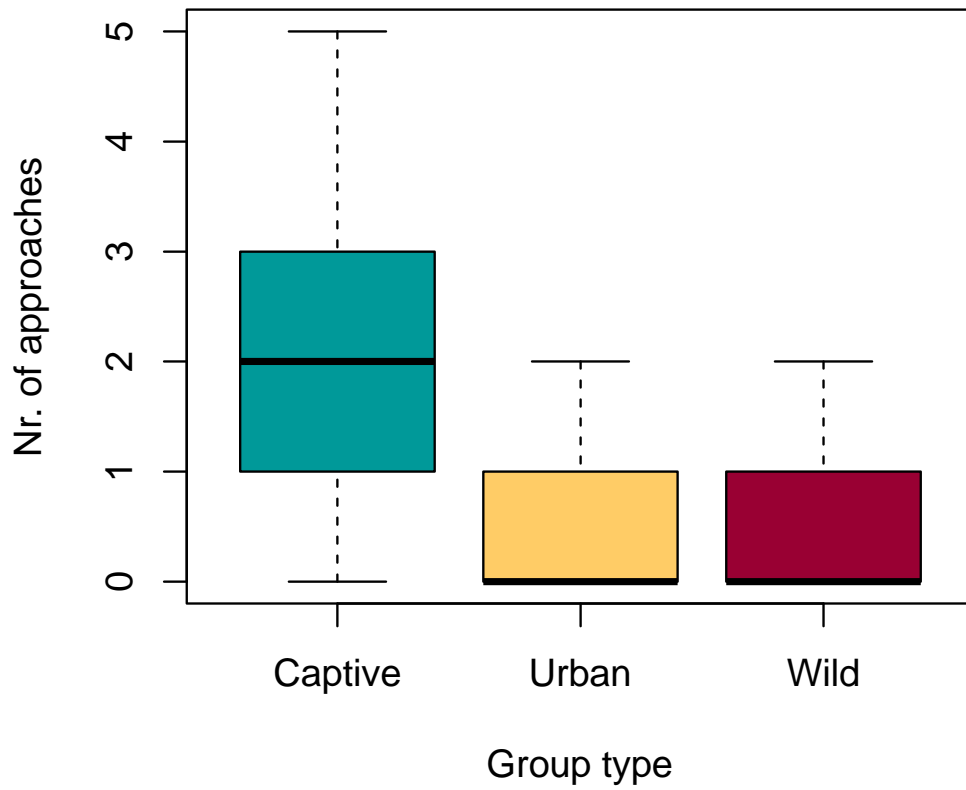Fig 1: Boxplots of the number of approaches performed by each group. Each point corresponds to an individual ($N_{captive} = 34$, $N_{wild} = 123$, $N_{urban} = 22$). Solid lines correspond to the group medians.
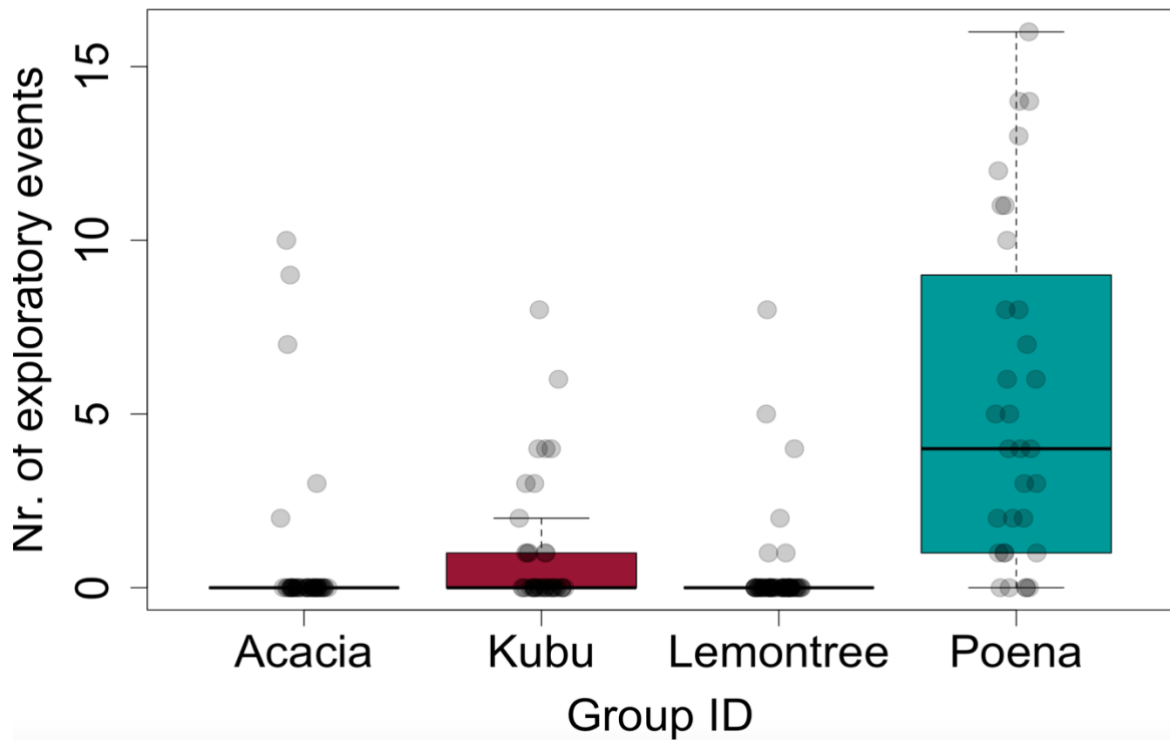
Fig 2: Boxplots of the number of exploratory events observed in each of the groups. The blue box corresponds to the captive group and the red box corresponds to a wild group.

Within the semi-urban group: effects of stimulus type, age and sex

Model 1a was overall significantly different from its corresponding null model (likelihood ratio test: X^2=31.98, df =16, p<0.004; R^2 full model= 0.92). Age and sex had a significant effect on the number of approaches to the novel stimuli, (age and sex: p=015). More specifically we found that juvenile males approached the novel stimuli significantly more times than other age classes and females. Model 1b was not significantly different from the null model (likelihood ratio test: X^2=13.9, df =11, p=0.09; R^2 full model= 0.2). However, in the model stimulus type had a significant effect on number of exploratory

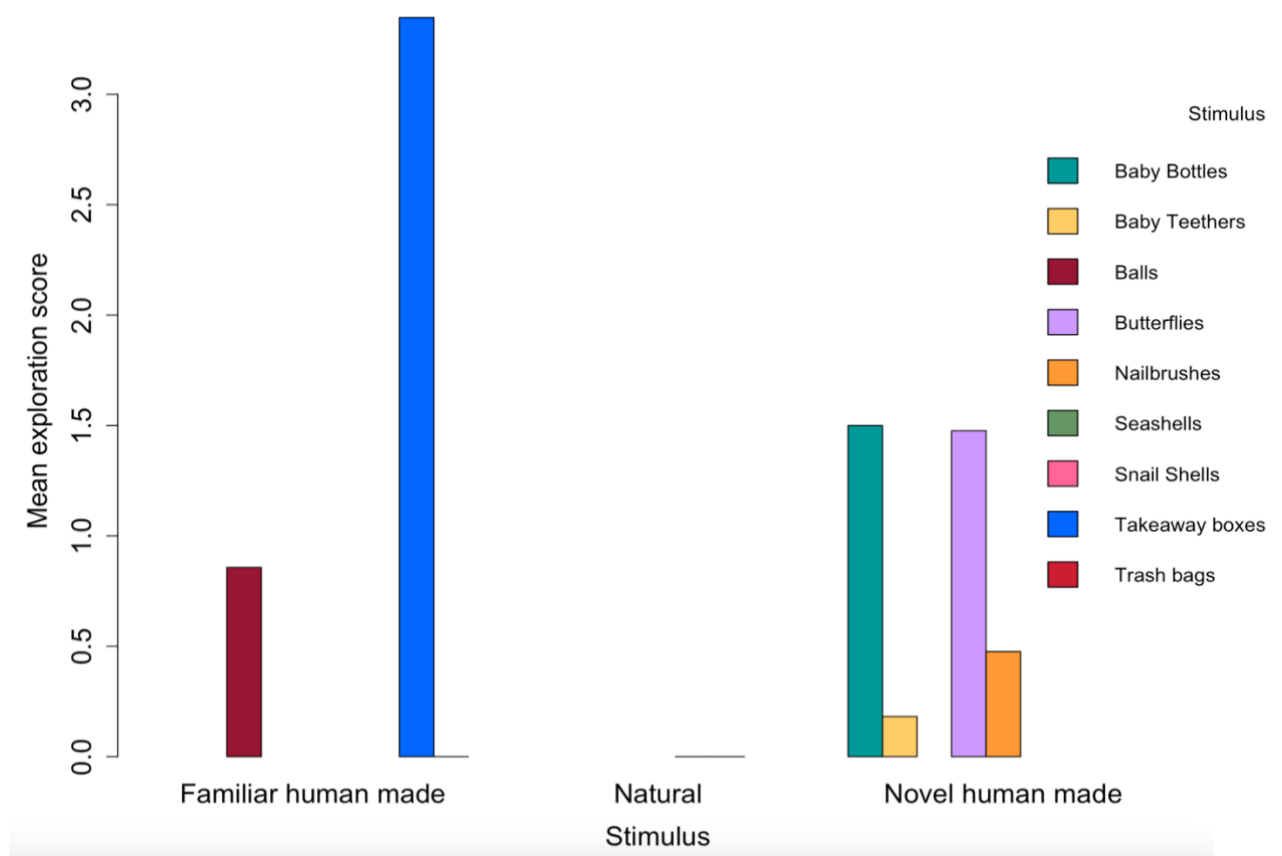events (plastic butterflies; p<0.002, takeaway boxes; p<0.0004, baby bottle; p<0.001 see fig 4).

Fig 3: Bar plot showing the mean exploration score (nr of exploratory events) for each stimulus presented to the semi-urban monkeys.

Individual level curiosity within captive, wild and semi-urban groups

Model 3a was overall significant according to the null model comparison (likelihood ratio test: X^2=16.48, df = 7, p = 0.003; R^2 full model = 0.71). We found that when the two variables (age category and sex) were combined they were significantly correlated with exploration score (p = 0.006, see fig 3). Specifically juvenile males were more explorative than the other age categories and sexes.
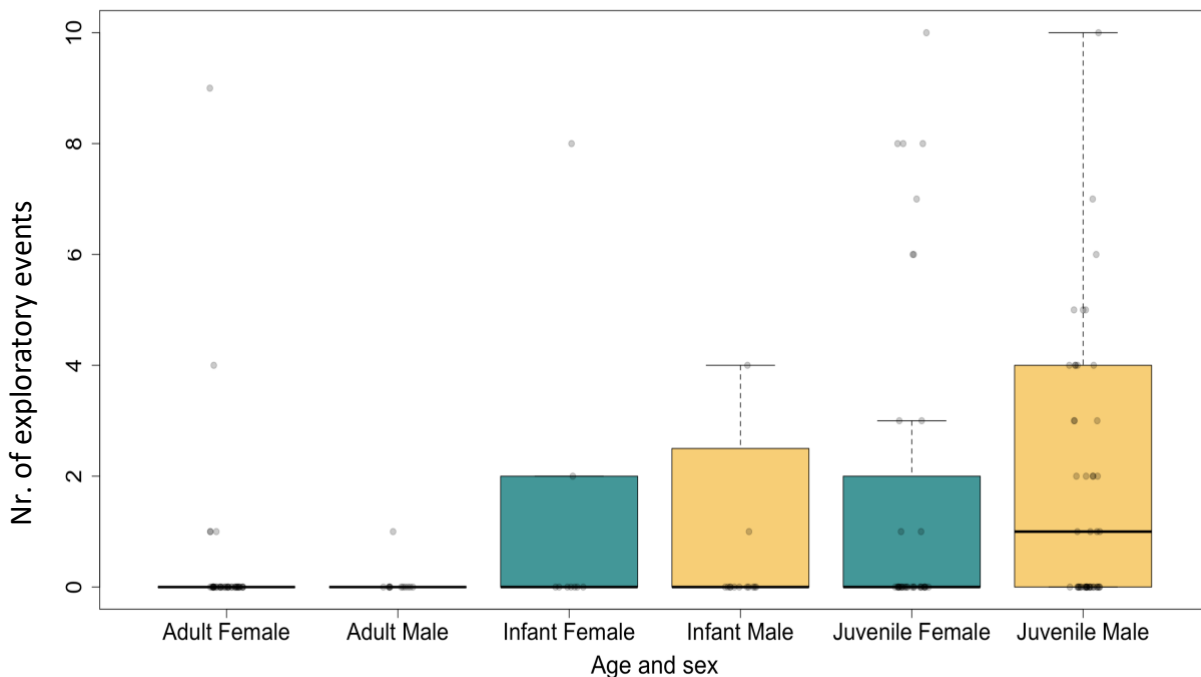
Fig 4: Boxplots showing the number of exploratory events for each age class and sex in all groups of monkeys.

Discussion

The present study aimed to investigate exploratory tendencies in vervet monkeys *(Chlorocebus pygerythrus)* living in different environments, including semi-urban, wild, and captive settings. By using novel-object paradigms, we examined the responses of vervet monkeys to novel stimuli and explored the potential effects of neophobia and curiosity on their exploratory behaviour.

As predicted, captive vervet monkeys exhibited the highest level of exploration behaviour among the three environments. This finding is consistent with previous research indicating that captive animals, due to a higher level of habituation to humans and a risk-free habitat, tend to exhibit reduced levels of neophobia and increased positive association with novelty (Forss et al. 2022). However, semi-urban monkeys likely have a higher level of habituation to humans than the wild monkeys. Therefore, the significant difference in exploratory behaviour between the captive and semi-urban monkeys is surprising as we expected a higher level of human habituation to have a positive influence on level of exploration (Forss 2022).

Contrary to our initial prediction, we did not observe a significant difference in interest in novelty between semi-urban and wild monkeys. This suggests that the semi-urban vervet monkeys, despite their exposure to an urban environment, did not show increased curiosity towards novel stimuli compared to their wild counterparts. This finding challenges the notion that neophobia and curiosity play a role in behavioural flexibility and suggests that other factors, such as habituation to humans and human artefacts, may play a more significant role in influencing their response to novelty. More precisely, this group of monkeys regularly enter human gardens and even within households, and thus it is possible that the high frequencies of semi-urban monkeys encountering all types of human artefacts has somewhat habituated them towards anthropogenic materials. Consequently, they may distinguish between different types of human made artefacts based upon their potential association to finding food in them. The higher exploration of take-away boxes and baby bottles indicate such effect.

The present study also examined the impact of different types of novel stimulus type on exploratory behaviour in semi-urban monkeys. Results revealed that the semi-urban monkeys did in fact have high levels of exploratory behaviour when presented with certain objects. We hypothesized that these monkeys, due to their regular exposure to human food sources, would show a greater interest in exploring objects associated with a potential food reward. Our findings partly supported this hypothesis, as the null model comparison was insignificant. The model however showed that semi-urban vervet monkeys exhibited a higher motivation to explore both takeaway boxes and baby bottles; objects we believe these monkeys potentially associated with food. Perhaps semi-urban monkeys are more explorative than wild monkeys when exposed to food related objects. However, plastic rubbish bags which were also assumed to be associated with food were not explored at all. This could suggest that consistent exposure to human artefacts and food items may influence foraging decisions and exploratory behaviour when presented with novelty. Moreover, this could potentially be due to the way we presented the bags; we did not put any items inside that could make them more attractive and vervet monkeys may rely on smell or a direct view of food items to be motivated to explore. Additionally, the exploration of the takeaway boxes could potentially be attributed to the material (Styrofoam). This material is easily ripped apart and chewed on and the juveniles exhibited a significant amount of playful behaviour with these boxes. Both the plastic butterflies and the baby

bottles were also significantly explored, both these items had something in common; they were colourful, more colourful than the other novel stimuli. Vervet monkeys like many other mammals are trichromatic, meaning they can see a large range of different wavelengths of light including red (Skalníková et al. 2020). The visual appeal of these objects may be an explanation for higher levels of exploratory behaviour with the more colourful stimuli.

Additionally, the inter-individual effects of age and sex were predicted to impact exploratory behaviour. Age was predicted to influence curiosity especially in the wild, and potentially in urban environments where exploring the unknown is related to risks, juveniles are expected to be curious, playful, and explorative to fill the need of learning about their environment (Fairbanks and McGuire 1993, Bergman and Kitchen 2009, Thornton and Samson 2012, Debeffe et al. 2013). On the other hand, since in most animal species juvenile mortality is higher than for adults, juveniles are also expected to be cautious and not engage in risky exploration (Struhsaker 1976, Fairbanks 1993, Isbell et al. 2009). Males as the dispersing sex, may tend to be more explorative than females as they are required to leave their natal group and search for a new group when sexually mature. We predicted that juveniles and males would show higher levels of motivation to explore novelty. Our results partially supported this prediction, as we found that juveniles, in general, exhibited more exploratory behaviour than adults. This can be attributed to their need to learn about their environment and acquire valuable information for survival. In contrast, the influence of sex on exploratory behaviour was not consistently observed. While male vervet monkeys are the dispersing sex, leaving their natal group at sexual maturity in search of a new group for breeding. Therefore, the need to explore unfamiliar environments is expected to be higher in males than females (Fairbanks and McGuire 1993, Bergman and Kitchen 2009, Thornton and Samson 2012, Debeffe et al. 2013). However, we did not find significant differences between males and females in their response to novelty, implying that traits necessary for dispersal and exploring new habitat areas may be distinct from curiosity directed towards novelty within a familiar environment. Future research with larger sample sizes may help elucidate the role of sex in vervet monkey exploration behaviour more accurately.

Study limitations

It is important to acknowledge some limitations of this study. Firstly, the number of groups studied was relatively limited, only one captive group and one semi-urban group were used in this study which may limit the generalizability of our findings. Future studies should include more groups across different habitats and varying levels of human habituation, to verify the effects motivational traits on novelty exploration (Forss et al., 2021). Additionally, the study focused on novel objects and did not include novel food items and due to previous experience with novel foods semi-urban groups may be more inclined to explore novel food items more than their wild conspecifics. In addition, social dominance is an important variable to consider in future research, higher ranking individuals tend to monopolize resources and thus may be more explorative than lower ranking members.

In conclusion, our study investigated the exploratory tendencies of vervet monkeys living in different environments and examined the interindividual effects of age and sex and stimuli type on their levels of exploration. The results challenge the notion that neophobia and curiosity play a significant role in adapting to novel environments. Findings also highlight the potential role of food association in shaping the cognitive and behavioural flexibility of semi-urban vervet monkeys. These findings contribute to our understanding of primate behaviour in changing environments and have implications for the management of human-wildlife interactions in urban areas. Further research in this area is warranted to deepen our knowledge of the cognitive processes underlying exploration tendencies in vervet monkeys and other primate species.

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