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Urbanization does not increase "object curiosity" in vervet monkeys, but semi-urban individuals selectively explore food-related anthropogenic items

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Abstract

Urban environments expose animals to abundant anthropogenic materials and foods that facilitate foraging innovations in species with opportunistic diets and high behavioral flexibility. Neophilia and exploration tendency are believed to be important behavioral traits for animals thriving in urban environments. Vervet monkeys (*Chlorocebus pygerythrus*) are one of few primate species that have successfully adapted to urban environments, thus making them an ideal species to study these traits. Using a within-species cross-habitat approach, we compared neophilia and exploration of novel objects (jointly referred to as "object curiosity") between semi-urban, wild, and captive monkeys to shed light on the cognitive traits facilitating urban living. To measure "object curiosity," we exposed monkeys to various types of novel stimuli and compared their approaches and explorative behavior. Our results revealed differences in the number of approaches and explorative behavior toward novel stimuli between the habitat types considered. Captive vervet monkeys were significantly more explorative than both semi- urban and wild troops, suggesting that positive experiences with humans and lack of predation, rather than exposure to human materials per se, influence object curiosity. Across habitats, juvenile males were the most explorative age-sex class. This is likely due to males being the dispersing sex and juveniles being more motivated to learn about their environment. Additionally, we found that items potentially associated with human food, elicited stronger explorative responses in semi-urban monkeys than non-food related objects, suggesting that their motivation to explore might be driven by "anthrophilia", that is, their experience of rewarding foraging on similar anthropogenic food sources. We conclude that varying levels of exposure to humans, predation and pre-exposure to human food packaging explain variation in "object curiosity" in our sample of vervet monkeys.

Key words: animal urbanization, neophilia, novelty response, object curiosity, vervet monkeys.

As natural habitats decline, animals must adapt to increasingly human-altered environments. One way for animals to cope with habitat transformation is to exploit newly available or previously unused resources (Greenberg 2003; Tuomainen and Candolin 2011; Nowak and Lee 2013; Sih 2013; Sol et al. 2013; Castano et al. 2023). Thus, at the species level, behavioral flexibility, innovation of new behaviors and rapid learning are key mechanisms to successfully adapt to novel resources (Lefebvre et al. 1997; Brooke et al. 1998; Estes et al. 1998; Berger et al. 2001). Whilst we know that many species can exploit anthropogenic resources through innovative extractive foraging techniques like bin foraging by common brushtail possums (*Trichosurus vulpecula*; Wat et al. 2020) and cockatoos (*Cacatua galerita;* Klump et al. 2021), or milk bottle-opening by blue tits (*Cyanistes caeruleus*; Lefebvre 1995), we know less about the cognitive and behavioral mechanisms explaining variation in behavioral innovation within species.

Species differ in traits like neophobia, neophilia and curiosity, which are necessary to gather new information and therefore can be decisive for adapting to new environments and exploiting new resources (Greenberg 1983, 1989, 2003; Mettke-Hofmann et al. 2002). Neophobia is avoidance of novel stimuli, whilst neophilia refers to a behavioral motivation that attracts animals to novelty (Greenberg 2003) and has been measured through novel object approaches across multiple animal taxa: rodent (Cowan 1977), primates (Bergman and Kitchen 2009), carnivores (Moretti et al. 2015), and birds (Castano et al. 2023; Inzani et al. 2023). Neophilia can thus lead to animals discovering novel beneficial resources, making it a critical behavioral trait in habitats characterized by rapid changes. Here, we use "object curiosity" as an umbrella term for neophilia (attraction to novelty) *combined with* exploration tendency (information gathering from novel objects by smelling, touching, and manipulating them), representing important underlying motivations of active learning (Tian et al. 2021).

Within species there are a myriad of factors causing variation in curiosity, such as the level of habituation to humans

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(Forss et al. 2022), age of individuals (Biondi et al. 2010), social context (Schaffer et al. 2021; Forss and Willems 2022), food abundance (Greenberg 1990; Mettke-Hofmann et al. 2002), competition (Greggor et al. 2016), and the environment (Johnson-Ulrich et al. 2021). Thus, we need to study these traits *within species, across contexts* to clarify the role they play in a species' adaptation to human-altered habitats.

Previous studies have shown that urban individuals are more likely to approach (i.e., neophilic) novel items than their rural or wild counterparts as for example in European blackbirds (*Turdus merula*; Miranda et al. 2013), great tits (*Parus major*; Tryjanowksi et al. 2016; Grunst et al. 2019), black-capped chickadees (*Poecile atricapillus*; Jarjour et al. 2020), red foxes (*Vulpes vulpes*; Padovani et al. 2021), and spotted hyenas (*Crocuta Crocuta*; Greenberg & Holekamp, 2017). But this pattern is far from universal (see reviews: Griffin 2022; Inzani et al. 2023). For example, in corvids it has been reported that the neophilia of urban birds is higher only in certain circumstances, due to experience with *specific items* (like litter) or even specific humans (Echeverría and Vassallo 2008; Greggor et al. 2016; Tryjanowski et al. 2016; Jarjour et al. 2020; Miller et al. 2022). These results suggest that urban areas in general can influence neophilia levels and animals can become accustomed to anthropogenic "novelty." Therefore, we must be careful in interpreting what is perceived as novel for the populations and individual animals residing within an urban habitat and start to disentangle general neophilia (attraction to novelty) from "anthrophilia." Here, we suggest the terminology "anthrophobia/ anthrophilia" to distinguish responses directed towards items/ foods that are associated with humans and/ or human habitats.

Primates are well known for their advanced behavioral flexibility and innovativeness (Kummer and Goodall 1985; Reader and Laland 2002; Hopper 2016; Ebel et al. 2019; Bandini and Harrison, 2020). We therefore expect the successful adaptation of primate species to human-altered environments to progress through innovative and flexible behavior (Schwitzer et al. 2011; Kalbitzer and Chapman 2018). Yet very few species of non-human primates thrive in the urban world due to their high conflict potential with humans (Siex and Struhsaker 1999; Beisner et al. 2015; Siljander et al. 2020). Further, for those primates that do successfully share their habitat with humans, we know very little about the extent to which behavioral traits are involved in their success. Urban primates therefore provide a great opportunity to gain insights in what role behavioral traits play in successful urban adaptation.

In this study, we investigated "object curiosity" in semi-urban, wild, and captive vervet monkeys using novel-object paradigms. Vervet monkeys present an interesting model species to investigate curiosity due to their 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) and are frequently in contact with human artifacts. Urban vervet monkeys are often described as problematic and a nuisance, and thus can experience negative treatments from humans, such as trapping and chasing. Captive monkeys, on the other hand, although also highly exposed to humans are being cared for and fed daily by them. Like monkeys in their natural habitat, urban populations are frequently exposed to high levels of risks, such as traffic, electric fences, and pets (Mikula et al. 2018). Given that vervet monkeys are highly adaptable and dietary generalists, one can assume generally low levels of neophobia and their behavioral repertoire to be characterized by a propensity for object neophilia and strong exploration tendencies (Greenberg 2003; Sol et al. 2011; Tryjanowski et al. 2016; Griffin et al. 2017; Barrett et al. 2019; Jarjour et al. 2020). Though at the species level, behavioral responses and the interest in novelty will reflect how individual animals perceive different stimuli depending on their past experiences (Moretti et al. 2015) and habitat influences (Birchmeier et al. 2023).

Here, we performed an intraspecific comparative study of "object curiosity" between vervet monkeys living in 3 different habitats: 1) a semi-urban anthropogenic habitat (defined as semi-urban due to the mosaic landscape of our study site consisting of natural vegetation as well as human constructions and residential areas; Pillay et al. 2023), 2) an undisturbed natural ecosystem (henceforth wild), and 3) captivity (wildlife sanctuary). First, we compared the responses to novel stimuli of semi-urban monkeys to those of wild and captive monkeys. We predicted that risk levels (which are high both in the semi-urban and the wild environments) will reduce curiosity in these groups compared with the captive population (Benson-Amram et al. 2013; Schaffer et al. 2021). We also predicted that human habituation would positively impact responses across all tested environments (Forss et al. 2022). Second, we investigated whether age and sex had any influence on the monkeys' response to novelty. Here, our prediction was that juveniles and males would be more motivated to explore novelty because they are more likely to phase situations when they need to learn more about their environment. Juveniles because they are less experienced relative to adults (Fairbanks 1993; Visalberghi et al. 2003) and males because they are the dispersing sex and can benefit more from interest in new opportunities and potential resources relative to females (Fairbanks and McGuire 1993; Bergman and Kitchen 2009; Thornton and Samson 2012; Debeffe et al. 2013). Third, using only the semi-urban troop, we evaluated potential effects of stimulus types ranging from human made to natural items. Due to their frequent exposure to a myriad of human artifacts, we predicted that vervet monkeys inhabiting anthropogenic environments would associate some objects such as takeaway boxes and trash bags with food and thus to be more anthrophilic to certain items due to potential access to food.

Materials and Methods

Subjects and study sites

We conducted field experiments on behavioral responses to novelty between January and March 2023 at the Urban Vervet Project (UVP), located in the Simbithi eco-estate in Ballito, KwaZulu-Natal, South Africa. The study site constitutes a private gated community with various housing and leisure areas and is home to multiple free-roaming troops of vervet monkeys. Because this study took place at the initial phase of UVP, only the individuals from one troop (Acacia, $N = 22$, which also resembled the actual groups size during our experiments) could be individually identified. The troop's previous history was unknown, but most monkeys were well habituated to human presence due to daily exposure at the eco-estate. The environment at Simbithi is defined as semi-urban due to a high degree of natural spaces within the eco-estate, in comparison with a city or suburb (Pillay et al. 2023).

We compared the data collected in this semi-urban vervet population to data previously collected on wild and captive vervet monkeys by SF between February and March 2020 at the Inkawu Vervet Project (IVP), located in the Mawana game reserve in KwaZulu-Natal, South Africa. This field site is home to several habituated vervet monkey troops that are continuously monitored and that regularly participate in experimental studies. The dataset analyzed here includes data from 2 of these wild troops (group size at the time of experiments: Kubu, $N = 19$ and lemon tree, $N = 24$) that were tested on identical stimuli as in the other habitats. The Kubu and lemon tree troops have been habituated since 2010. However, not all monkeys were always present during the experiments, therefore our analyses included only the monkeys present during the experiments (Kubu, $N = 12$ and lemon tree, $N = 13$). Data from one wild unhabituated troop (Congo) is included in this manuscript but not in the statistical analyses due to lack of individual-level data.

Data on captive vervet monkeys was collected at the Wild Animal Trauma Centre & Haven (WATCH) vervet sanctuary in Vryheid, KwaZulu-Natal, South Africa. From the WATCH sanctuary data, one group was included in this study (group size at time of experiments: Poena, $N = 17$, actual number of monkeys present during experiments $N = 11$). Many of the monkeys in this sanctuary have been cared for by humans because 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-fed. At 3 months of age, they are gradually integrated into a troop of conspecifics.

All group compositions encompassed both male and female individuals across diverse age categories: infants (up to 1 year old), juveniles (ranging from 1 to 3 years for females and 4 years for males to account for sexual dimorphism), and adults (aged 4 years and older). Only individuals for which age, sex, and rank was known were included in models 1a and 1b (sample sizes are reported in Tables 3–6). For adults, rank was calculated using Elo-rating methods based on agonistic conflicts to create a matrix of winner-losers (Neumann et al. 2011). For juveniles, we gave them the score just below their mothers after the literature reporting linear dominance hierarchies in vervet monkeys so that offspring inherit the rank of their mothers (Young et al. 2017; Jarrett et al.2018).

Experimental setup

To compare behavioral responses to different novel items across habitat types (captive, semi-urban, and wild), data was collected after the protocol described by Forss et al. (2022). For comparisons, we exposed the semi-urban monkeys at Simbithi with 2 identical novel stimuli that had been used in the previous study: seashells and plastic butterflies. The stimuli were presented in the same order in all habitat types to control for potential order effects. The plastic butterflies were of different colors than natural existing butterflies within the habitat of either the wild or the semi-urban monkeys and seashells are not naturally present within any of the habitats. As such, these novel items present stimuli that are relatively close to natural occurring items, yet still new to the monkeys. To evaluate the effect of food-associated stimuli on behavioral responses, we also presented the semi-urban troop with 6 other stimuli representing various distinct materials, colors, and familiarity: 3 human-made and familiar to this population (trash bags, balls, and takeaway boxes), and 3 human-made less encountered "novel" items (nailbrushes, baby bottles, and baby teethers). For the semi-urban and wild troops, all experiments were conducted in familiar and safe areas to the monkeys where they were observed napping and sleeping and that had low grass coverage for better visibility. For the captive troop, experiments were performed in their outdoor enclosure where they spend their time on daily basis. The outdoor enclosure was composed of multiple larger compartments and climbing structures and was neighboring 2 other outdoor enclosures with monkey troops present, thus monkeys of the tested Poena troop could experience social disturbance from neighboring troops during testing.

A stimulus was presented only once and only one stimulus was presented per day with a minimum of one day between experiments. 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). We placed 12 copies of each stimulus 1 m apart to reduce monopolization of objects by dominant troop members. All novelty exposures lasted for 20 min so that low-ranking individuals could receive access to the new items even if the dominant individuals approached first. The 20 min was enough time to give all monkeys who wanted to approach the opportunity to do so. Only in one exceptional case did the experiment run 26 min instead of 20 (Seashell exposure in Acacia) because in this case a low-ranking individual joined the group later and thus, we wanted to provide the same opportunity for that individual to interact with the items.

To replicate the procedure of the experiments done with the wild and captive troops (Forss et al. 2022), and to attract the attention of the monkeys to the experimental grid, a handful of soaked corn was placed in the middle of the area where the items were placed. Two weeks before conducting the experiments, we tested the monkeys with a small amount of corn to confirm that it was a desirable food source also for the semi-urban population. During experiments in the wild and the semi-urban environments, 2 human observers were observing and identifying the monkeys within 10–20 m of the experimental grid. For the captive troop, 2 humans were video recording from outside the outdoor enclosure with a minimum 5 m to the monkeys but with a mesh separating them.

The data extracted from the videos of the experiments included number of approaches (within 5 m of the stimuli) and number of exploration events (touching, sniffing, lifting, chewing, and manipulating) toward the presented items. We video-recorded all experiments with 2 Sony cameras HDR-CX200, one mounted on a tripod and the other held by an observer zooming in on any explorative behavior.

Video coding and measurements

All behaviors were identified and coded from video recordings using the video coding software Cowlog. The number of approaches was determined by the number of times each monkey made an approach within 5 m of any of the presented items. Once a monkey made physical contact with an object, we coded the number of exploratory events directed toward the objects (manipulations, sniffs, tastes, chews, and the number of times an item was moved/lifted). We then summed these behaviors into one exploration score. We assessed inter-observer reliability using the unweighted Cohen's Kappa method in R using the package irr (Gamer et al., 2019). Observers LE and SM independently rated 33% of the same video recordings and the resulting Cohen's Kappa score

was calculated to be 0.823, indicating substantial agreement between observers.

Statistical analyses

We conducted the statistical analyses in R (version 4.3.0; R Core Team, 2023) and RStudio (R Core Team 2023). We built 4 different generalized linear mixed models (GLMM) to analyze our data using the packages lme4 (Bates et al. 2015, Model 1a and 1b) and the package glmmTMB (Brooks et al. 2017, Models 2a and 2b). We checked all models for overdispersion using the function check overdispersion from the package performance (Fox and Weisberg 2019) and overall stability with the package DHARMa (Hartig 2020). We drew inference by comparing the full model with a null model lacking predictors of interest but containing 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 2 models (1a and 1b, see Tables 1 and 2) included as response variables the number of approaches (Model 1a, Poisson model) and exploration score (Model 1b; Poisson model) of the individual monkeys, respectively. In both models, we tested the effect of habitat type (3 levels: captive, semi-urban, and wild), stimulus type (2 levels: butterflies and seashells, the 2 objects that were "novel" to all the monkeys in each habitat type), their interaction and rank (3 levels: low, middle, and high). Additionally, to capture the potential interaction between age and sex, we created a new variable, age.sex, by combining information on age (3 levels: infant, juvenile, and adult) and sex (2 levels: female and male). The interaction effect is implicitly represented in this composite variable, allowing us to assess how the relationship with the dependent variable may vary based on different combinations of age and sex. As random effects, we included individual ID nested within Group ID, and group size was included as an offset to account for the different numbers of individuals in the different groups.

The second set of models (2a and 2b, see Tables 1 and 2) only included data from the semi-urban troop (referred to as urban in the results for simplicity). In these models, we investigated the effects of stimulus type (9 levels: seashells, butterflies, nailbrushes, baby bottles, trash bags, balls, take-away boxes, baby teethers, and snail shells), on individual exploration scores (Model 2a, Poisson model) and the number of approaches to the novel stimuli performed by each individual (Model 2b, negative binomial model). Both models included the random intercept of individual ID. Additionally, we calculated the number of exploration events for the unhabituated wild group (Congo) but did not include this group in the analyses as the monkeys were unhabituated and not individually identified. Post hoc pairwise comparisons were conducted using the function emmeans from the package of the same name (Lenth 2023).

Results

Neophobia and object curiosity across habitats

In Model 1a we tested whether the number of approaches to novel stimuli was influenced by habitat types, the stimulus presented, individual rank, sex, and age. We found that the

Table 1. Overview of the different models addressing how habitat and stimulus type influence object curiosity in vervet monkeys and the models' response variables, fixed and random effects, and population sample used

Model	Response	Fixed	Random	Population
1a—Habitat types	Number of approaches	Group type * stimulus + age.sex + rank	Group ID/ Individual	Captive, semi-urban, wild
1b—Habitat types	Exploration score	Group type * stimulus + age.sex + rank	Group ID/ Individual	Captive, semi-urban, wild
2a—Urbanization	Number of approaches	Stimulus	Individual	Semi-urban
2b—Urbanization	Exploration score	Stimulus	Individual	Semi-urban

Table 2. Summary of the different stimuli used to measure object curiosity in vervet monkeys in the different habitat types: captive, semi-urban, and wild

Stimuli	Type	Used	Included in models	Number of individuals present during testing
Butterflies	Naturalistic Human-made Novel	Captive, semi-urban, wild	1a, 1b, 2a, 2b	57
Seashells	Natural Novel	Captive, semi-urban, wild	1a, 1b, 2a, 2b	57
Nailbrushes	Human-made novel	Semi-urban	2a, 2b	22
Baby bottles	Human-made familiar	Semi-urban	2a, 2b	22
Trash bags	Human-made familiar	Semi-urban	2a, 2b	22
Balls (ping-pong/golf)	Human-made familiar	Semi-urban	2a, 2b	22
Take away boxes	Human-made familiar	Semi-urban	2a, 2b	22
Baby teethers	Human-made novel	Semi-urban	2a, 2b	22
Snail shells	Natural familiar	Semi-urban	2a, 2b	22

model was overall significantly different from the null model (likelihood ratio test (LRT): $\chi^2 = 27.48$, df = 9, $P = 0.004$; R^2 full model = 0.94.) The interaction between habitat types and stimulus was not significant (LRT = 3.93, $P = 0.14$) and we therefore refitted the model without the interaction to evaluate individual effects of habitat type and stimulus. Single-term deletions of habitat type, stimulus, and rank showed no significant effect of these variables on monkeys' number of approaches to the novel stimuli (habitat type: LRT = 4.60, $P = 0.10$; stimulus: LRT = 0.57, $P = 0.45$; rank: LRT = 2.11, $P = 0.35$ see Table 1 for model estimates and P values). However, P values calculated via model summary and pairwise comparisons corrected for multiple testing revealed that captive individuals approached significantly more often novel stimuli than urban and wild individuals (contrast captive-urban: estimate = 1.40, SE = 0.48, $P = 0.009$; captive-wild: estimate = 0.91, SE = 0.399, $P = 0.05$; urban–wild: estimate = –0.48, SE = 0.43, $P = 0.50$; see also Table 3 and Figure 1). Furthermore, although we could not statistically test how the number of approaches of wild unhabituated individuals compared with the other habitat types, a qualitative comparison revealed that the wild unhabituated troop (Congo) had the lowest mean individual number of approaches among monkeys in the different habitat types (captive = 34, wild habituated = 13.5, urban = 14, wild unhabituated = 5). The combined age.sex variable had a significant effect on the response (LRT = 13.14, $P = 0.01$), with juvenile males being the age group that more often approached the novel stimuli, see Figure 2).

In Model 1b we tested whether exploratory behavior was influenced by habitat type, stimulus, individual rank, age, and sex. We found that the model was overall significantly different from the null model (LRT: $\chi^2 = 98.33$, df = 11, $P < 0.0001$, Table 4). The interaction between habitat type and stimulus was significant (LRT = 59.65, $P < 0.001$) whereas rank or the combination of age and sex were not (rank LRT = 0.93, $P = 0.62$; age.sex LRT = 8.01, $P = 0.09$, Figure 3). The exploration score of captive monkeys toward butterflies was found to be significantly higher than toward seashells, and higher than that of wild monkeys toward butterflies and seashells and of urban monkeys toward butterflies (Figure 3, Supplementary Table S1). Furthermore, captive monkeys also explored seashells more than wild monkeys explored butterflies (Figure 3, Supplementary Table S1). As before, we qualitatively compared the exploration score of wild unhabituated individuals with the individuals in the other habitat types and found that the wild unhabituated individuals had the lowest mean individual exploration score (mean individual exploration scores among monkeys at the different habitat types: captive = 147.5, wild habituated = 42.5, urban = 31, wild unhabituated = 2).

Factors affecting object curiosity within the semi-urban group

In Model 2a we tested whether the type of stimuli affected the number of approaches in the urban group (Acacia). This model was not overall significantly different from its corresponding null model (likelihood ratio test: $\chi^2 = 12.17$, df = 9, $P = 0.2$, Table 5).

In Model 2b we tested whether the type of stimuli affected the exploratory behavior of urban monkeys. We found that the model was overall significantly different from the null model (likelihood ratio test: $\chi^2 = 39.55$, df = 9, $P < 0.001$), with stimulus having a significant effect on exploratory behavior and takeaway boxes being explored the most on average (average exploration score: 3.3, Table 6).

Discussion

The present study investigates object curiosity in vervet monkeys from 3 different habitat types: captive, semi-urban, and wild. Using novel-object paradigms, we examined

Table 3: Summary of Poisson generalized linear mixed-effects model without interaction between habitat type and stimulus (Model 1a)

	Number of approaches		
Predictors	**Incidence rate ratios**	***CI***	***P***
(Intercept)	0.08	0.03–0.20	**0.001**
Environment [urban]	0.25	0.10–0.63	**0.004**
Environment [wild]	0.4	0.18–0.87	**0.022**
Stimulus [seashells]	0.87	0.61–1.24	0.451
age sex [adult.male]	0.79	0.22–2.87	0.725
age sex [infant.male]	0	0.00—Inf	0.998
age sex [juvenile.female]	1.67	0.84–3.31	0.145
age sex [juvenile.male]	2.14	1.12–4.09	**0.021**
Rank [low]	0.74	0.47–1.17	0.193
Rank [middle]	1.04	0.67–1.60	0.872
Random effects			
σ^2	3.03		
$\tau_{00\ \text{Individual:group.ID}}$	0		
$\tau_{00\ \text{group.ID}}$	0.07		
$N_{\text{Individual}}$	57		
$N_{\text{group.ID}}$	4		
Observations	108		
Marginal R^2/conditional R^2	0.821/ NA		

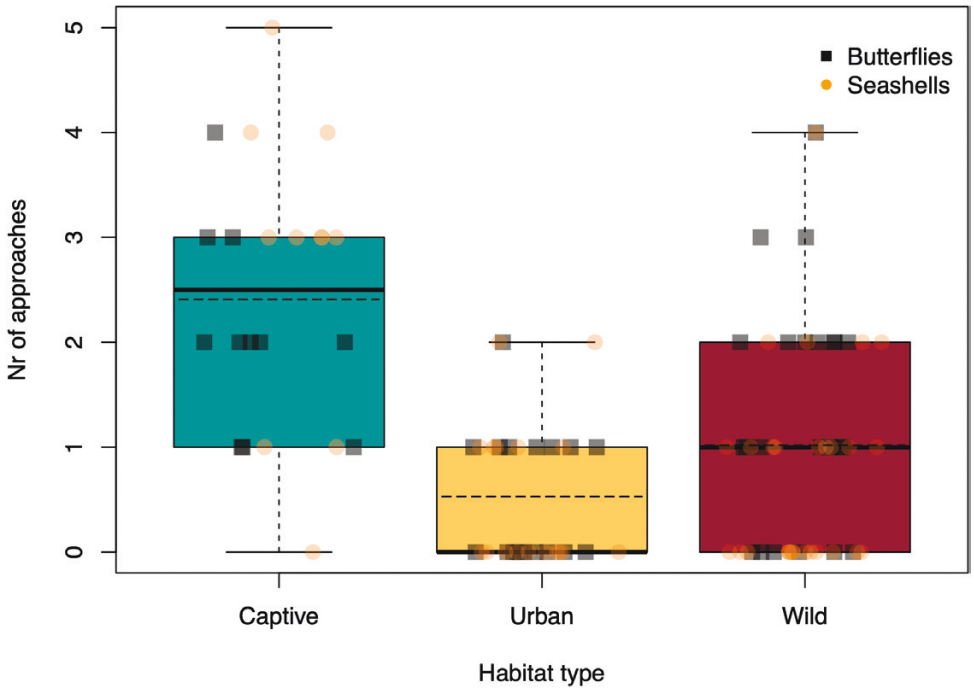

Figure 1. Boxplots of the average number of approaches performed by vervet monkeys in 3 different habitats (captive, semi-urban, and wild) to each of the 2 novel stimuli (butterflies and seashells). Solid horizontal lines correspond to the group medians and dashed horizontal lines correspond to group means.

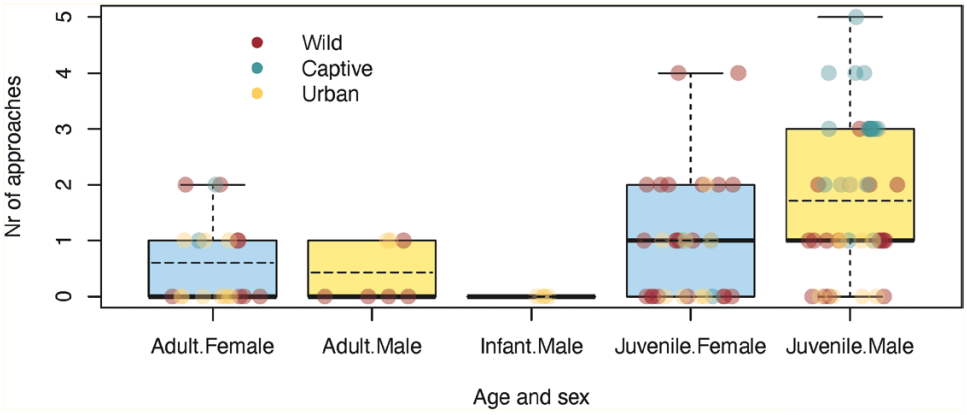

Figure 2. Boxplots showing number of approaches of vervet monkeys of different age and sex classes tested in the 3 habitat types: captive, semi-urban, and wild. Solid horizontal lines correspond to the group medians and dashed horizontal lines correspond to group means. Yellow boxes represent males while blue boxes females. Note that category Infant. Female is missing due to incomplete sample.

within-species variation in behavioral responses to a variety of items, as well as which factors impact object curiosity in this species.

Across the different habitats, as predicted, captive vervet monkeys exhibited the lowest neophobia (most approaches) and the highest level of exploratory behavior. This result is consistent with previous findings showing that captive animals that experience close exposure to humans within a risk-free habitat exhibit reduced levels of neophobia and increased positive associations with novel artifacts (Forss et al. 2022; Horn et al. 2022; Birchmeier et al. 2023). An additional contributing factor to the stronger object curiosity of captive monkeys could be the increased time available in their activity budget. Food is supplied to them, so they do not have to spend time searching for it. In addition, they may view any provided objects as enrichment. Both the plastic butterflies and seashells were new to this captive troop and regardless of stimulus type, the captive monkeys explored them more supporting the idea that any object is perceived as enrichment to them.

The semi-urban monkeys at our study site share their habitat with human residents and are daily exposed to human artifacts. Consequently, one would expect the semi-urban troop to show a higher level of exploration tendency compared with their wild counterparts. Yet, with the 2 stimuli tested across habitats, we found no significant differences in neither the number of approaches towards novel objects nor in exploration tendency between the semi-urban and the wild monkeys. Thus, living in an anthropogenic habitat did not result in higher approach frequency or exploration of objects

Table 4: Summary of Poisson generalized linear mixed-effects model (Model 1b). Note that the estimate of the effect of the urban environment on the exploration of seashells presented a large estimate error given that no exploration events were observed in these trials

	Exploration score		
Predictors	**Incidence rate ratios**	***CI***	***P***
(Intercept)	0.12	0.03–0.53	**0.005**
Environment [urban]	0.13	0.04–0.44	**0.001**
Environment [wild]	0.05	0.02–0.15	**0.001**
Stimulus [seashells]	0.32	0.20–0.50	**0.001**
age sex [Adult.Male]	0.29	0.01–5.71	0.414
age sex [Infant.Male]	0	0.00–Inf	0.999
age sex [Juvenile.Female]	2.58	0.68–9.78	0.165
age sex [Juvenile.Male]	2.11	0.59–7.56	0.254
Rank [low]	1.35	0.52–3.56	0.539
Rank [middle]	1.65	0.57–4.78	0.356
Environment [urban] × Stimulus [seashells]	0	0.00–Inf	0.996
Environment [wild] × Stimulus [seashells]	7.18	3.42–15.09	**0.001**
Random effects			
σ^2	3.42		
$\tau_{00\ \text{Individual:Group.ID}}$	1.47		
$\tau_{00\ \text{Group.ID}}$	0		
$N_{\text{Individual}}$	57		
$N_{\text{Group.ID}}$	4		
Observations	108		
Marginal R^2 /conditional R^2	0.958/NA		

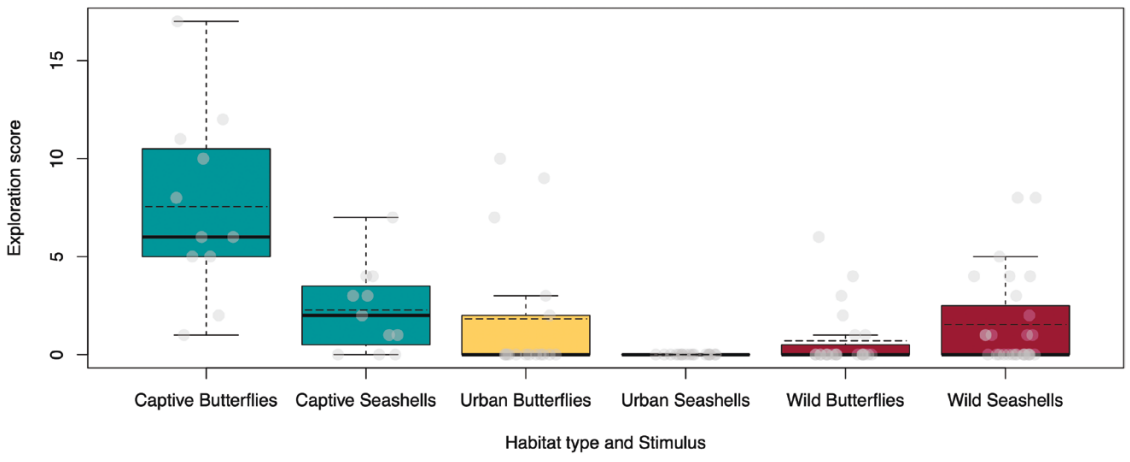

Figure 3. Boxplots showing the exploration scores of individual vervet monkeys in each habitat type (captive, urban, and wild) and stimulus presented. Solid horizontal lines correspond to the group medians and dashed horizontal lines correspond to group means.

per se. If a higher level of habituation to humans and their artifacts drives object curiosity, one would expect such a difference because *habituated* wild monkeys show increased object exploration compared with wild *unhabituated* monkeys (Forss et al. 2022). The lack of differences between semi-urban and wild monkeys could be due to higher-than-expected curiosity levels in the wild monkeys of our study, a lower-than-expected level of curiosity in semi-urban monkeys, or both. The wild habituated monkeys within our data set (Kubu and lemon tree troops) were very habituated to human researchers as they regularly participate in cognitive tasks involving human-made artifacts. Therefore, the habituation level of the wild troops might have been higher than what we predicted. Supporting this hypothesis, the wild unhabituated group did in fact present the lowest mean total number in object neophilia and exploration of all groups considered, meaning that the habituation level among the wild groups was not homogeneous, confirming the previous findings from Forss et al. (2022). A lower-than-expected curiosity level in the semi-urban monkeys could be due to overexposure

Table 5. Summary of Poisson generalized linear mixed-effects model (Model 2a) describing the number of approaches by semi-urban vervet monkeys to a variety of human made stimulus types. Note the extra 2 individuals counted in this model represent unidentified infants in the group

	Number of approaches		
Predictors	**Incidence rate ratios**	**CI**	***P***
(Intercept)	0.31	0.15–0.67	**0.003**
Stimulus [baby teethers]	1.21	0.50–2.93	0.673
Stimulus [balls]	0.35	0.09–1.28	0.113
Stimulus [butterflies]	1.04	0.41–2.63	0.932
Stimulus [nailbrushes]	1.39	0.58–3.30	0.457
Stimulus [seashells]	1.16	0.47–2.85	0.751
Stimulus [snail shells]	0.44	0.14–1.43	0.173
Stimulus [takeaway boxes]	1.54	0.67–3.54	0.305
Stimulus [trash bags]	0.87	0.33–2.27	0.778
Random effects			
σ^2	1.42		
$\tau_{00\ Individual}$	0.59		
ICC	0.29		
$N_{Individual}$	24		
Observations	196		
Marginal R^2/conditional R^2	0.103/0.366		

Table 6. Summary of Poisson generalized linear mixed-effects model (Model 2b) describing explorative behaviors by the semi-urban vervet monkeys for a variety of stimulus types. Note the extra 2 individuals counted in this model represent unidentified infants in the group

	Exploration score		
Predictors	**Incidence rate ratios**	**CI**	***P***
(Intercept)	2.93	1.19–7.20	**0.019**
Stimulus [baby bottles]	0.13	0.03–0.60	**0.009**
Stimulus [baby teethers]	0.12	0.03–0.57	**0.007**
Stimulus [balls]	0.13	0.03–0.60	**0.009**
Stimulus [butterflies]	0.42	0.15–1.22	0.11
Stimulus [nailbrushes]	0.2	0.05–0.74	**0.016**
Stimulus [seashells]	0	0.00–Inf	0.999
Stimulus [snail shells]	0	0.00–Inf	0.999
Stimulus [trash bags]	0	0.00–Inf	0.999
Random effects			
σ^2	3.07		
$\tau_{00\ Individual}$	0.86		
ICC	0.22		
$N_{Individual}$	24		
Observations	196		
Marginal R^2/conditional R^2	0.959/0.968		

to human artifacts. The Simbithi monkeys regularly enter human gardens and households, and the high frequencies of them encountering all types of human artifacts may have habituated them towards anthropogenic materials to the extent that they ignore them. The fact that the semi-urban monkeys explored butterflies more and basically left seashells untouched suggest that they may have been familiar with seashells potentially from entering bathrooms and houses featuring such decorations. Wild monkeys on the other hand had certainly never encountered seashells and responded with higher exploration scores of seashells compared with the semi-urban ones, indicating the curiosity towards seashells in wild monkeys reflects the perception of novelty.

The similarity between wild and semi-urban groups could further be explained by the fact that, just like their wild peers, semi-urban monkeys experience a magnitude of risks within their habitat. There are natural predators like raptors and pythons within the Simbithi eco-estate and monkeys here face the additional threats of cars, dogs, and human hazards, like snares that are apparent just outside the estate, yet within the home range of our study troop. Thus, the low object curiosity of both semi-urban and wild (habituated) monkeys may

derive from the risks both environments pose, selecting for similar levels of neophobia and caution towards novelty. This in turn leads to monkeys in these 2 habitats not eagerly engaging in risky exploration, in contrast to the captive conspecifics freed from such potential risks (Lowry et al. 2013; Vincze et al. 2016). As such, our findings suggest that factors beyond direct anthropogenic exposure may influence the exploratory behavior of vervet monkeys.

Our second set of models revealed that semi-urban monkeys distinguish between different types of human-made artifacts based on the potential to find food in them, with take-away boxes being the most explored stimuli. Thus, shows anthrophilia rather than neophilia toward random objects. The higher exploration of butterflies (monkeys occasionally catch and eat natural butterflies, as well as some caterpillars), take-away boxes, and baby bottles indicate such an effect. However, somewhat puzzling, plastic rubbish bags which also presumably can be associated with food were not explored at all. This could potentially be due to the way we presented the bags; we did not put any food 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. The increased exploration of the takeaway boxes also cannot be explained by order of presentation as this stimulus type was presented on the 7th day of experiments out of the 10 categories (Supplementary Material). As such, we hypothesize that consistent exposure to human artifacts and food items may influence foraging decisions and exploratory behavior when encountering different items in different contexts, and that vervet monkeys selectively explore food-related anthropogenic items more.

Across all 3 habitats, we found that juvenile males exhibited more exploratory behavior than adults. This age difference aligns with previous findings from various species (Biondi et al. 2010; Castano et al. 2023) as 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, because in most animal species juvenile mortality is higher than for adults, juveniles are also expected to be cautious and not engage in risky exploration before reproductive age is reached (Struhsaker 1976; Fairbanks 1993; Isbell et al. 2009). As such, in natural and semi-urban environments, exploring the unknown is related to risks, and thus individuals must balance the risk-reward trade-off (Houston et al. 1997; Sih and Del Giudice 2012; Mazza et al. 2019). Our data shows that in vervet monkeys, juvenile males showed the highest levels of motivation to approach novel objects. In vervet monkeys, males are the dispersing sex, leaving their natal groups as they reach sexual maturity and dispersing multiple times throughout their life (Young et al. 2019). Consequently, our data is suggestive that they may have a higher predisposition for explorative behaviors than females because they are required to adjust to novel situations, such as potential new foraging situations (Cheney and Seyfarth 1983; Blaszczyk 2017).

It is important to acknowledge some limitations of this study. First, the number of troops studied was limited, only one captive and one semi-urban troop were used in this study which may limit the generalizability of our findings. Future research with larger sample sizes may help disentangle the role of sex and social rank in vervet monkey exploration behavior to that from risk-taking propensities more accurately.

In conclusion, this study offers a nuanced perspective on object curiosity in vervet monkeys across diverse habitats. The results challenge prevailing assumptions about the role of neophilia in urban adaptation, highlighting the importance of habituation to humans and human-associated stimuli. In other words, "anthrophilia" may be more influential in shaping vervet monkeys' responses to novel objects. The age and sex differences observed contribute to our understanding of individual variation in exploration behavior, emphasizing the need for continued research to untangle the intricate interplay between motivational traits and environmental adaptation in non-human primates.

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Conflict of Interest statement

The authors declare that they have no conflict of interest.

Authors' Contributions

L.E. collected the data at Simbithi Eco Estate, analyzed results and wrote the initial work as her master's thesis, S.M.: data collection, supervision, editing of manuscript, A.M.R.: analyzed results and wrote the manuscript, E.v.W.: collaboration with the data collected at Inkawu Vervet Project, S.F.: study conceptualization, collected the data set on wild and captive monkeys, supervision, acquired funding and wrote the manuscript.

Ethics Statement

This study was based solely on behavioural observations and non-invasive methods with severity degree zero. All experiments complied with the ethical principles set by the Animal Research Ethics Committee (AREC) at the University of Kwazulu-Natal, South Africa; ethical approval number T20220164.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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