The Role of Umwelt in Animal Curiosity: A Within and Between Species Comparison of Novelty Exploration in Mongooses

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Abstract – In its broadest sense, curiosity has been described as an intrinsic motivation to acquire novel information; this 'novelty-seeking' is notably in the absence of any immediate reward. One way to examine information seeking in animals, has been to present animals with novel objects and measure the way animals gather information through exploration. While this is a standardized and common paradigm, few studies have focused on *what factors* influence how animals *perceive novelty,* whilst considering the predicted impacts of an animal's 'umwelt' on exploration. In this study we assessed explorative behaviors in mongooses through both an intra and interspecific view. First, in meerkats (*Suricata suricatta*) tested in their natural environment, we established that they distinguish familiar from unfamiliar and show increased exploration of novel objects. We also found that odor influenced the meerkats' explorative action, so that non-odorous items were manipulated longer. Presence of conspecifics influenced approaches to novelty, but not the exploration per se. Human presence interacted with an individual's level of habituation to impact approaches and exploration of novelty and we found a strong captivity effect on exploration between captive and wild meerkats. Between species analysis showed that yellow mongooses (*Cynictis penicillate*), a less social mongoose than meerkats, showed higher levels of novelty exploration, when tested within the same habitat. Thus, these findings show that multiple factors, including perceptual abilities (merkwelt) and social factors (sozialwelt), are decisive for when and how animals explore their environment and must be considered both when designing novelty paradigm tests and their interpretations.

Keywords – Novelty response, Information seeking, Exploration, Animal curiosity, Meerkats, Yellow mongoose

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The way animals perceive and react to new information reveals insights to their basic cognitive processes and can help us understand biological contexts that promote curiosity and information seeking. In contrast to humans, where much research on our "intellectual curiosity" have been done through verbal assessments of subjects participating in studies through experiments and questionnaires (Dubey et al., 2021; Eschmann et al., 2022; Fandakova & Gruber, 2021; Gross et al., 2020), in animals, assessments of information seeking, or "observable curiosity," is limited to an animals' explorative or play behavior (Berlyne, 1966; Marsh, 2019; Pisula, 2020; Rojas-Ferrer et al., 2020). Introducing and exposing animals to a novel stimulus has become a prevailing paradigm to induce explorative and information seeking behaviors. This 'novel stimulus' paradigm has already been used across all major animal taxa: fish (Bisazza et al., 2001; Grill et al., 2012), amphibians (Carlson & Langkilde, 2013; Kelleher et al., 2018), reptiles (Bashaw et al., 2016; Siviter et al., 2017), various mammals (Bergman & Kitchen, 2009; Blaser & Heyser,

2015; Carter et al., 2018; Powell et al., 2004) and birds (Huber et al., 2001; Mettke-Hofmann et al., 2006; Miller et al., 2022; Stöwe et al., 2006). However, *how animals respond to novel stimuli* is critically dependent on the risk-reward trade-off with regards to gathering information. This trade-off is strongly affected by the interaction between the *properties of the novel stimuli* and the *characteristics of individuals and their environment*s - proximate, developmental, and evolutionary (i.e., their *umwelt*).

Species differ widely in their perceptual capacities due to differently evolved sensory channels (i.e., their *merkwelt*). Accordingly, *what information is* and *how it is collected* will depend highly on a species senses like sight, hearing, smell, and manipulative skills (Berlyne, 1966; Bueno-Guerra, 2018; Pisula, 2020). One assumption of novel stimuli paradigms is that animals can recognize something as "novel" and should thereby express different behavioral reactions to novel and familiar stimuli. When a stimulus is new it is expected to trigger an animal's information-seeking behavior. During this process of information gathering, the interaction between an animal's sensory abilities and the properties of the new stimulus likely affects the behavioral reaction. For example, something that omits a strong odor may provide the animal with new information even from a distance, especially for species with highly evolved olfaction. Consequently, in such situations "perceptual exploration" (Berlyne, 1966) can take place without physically interacting with the novel stimulus. Likewise, for large or visually distinctive stimuli, animals can seek information from visual exploration. Hence, for animals, the information-seeking process likely starts with a risk assessment and following behavioral response will depend on whether the animal perceives the new information as a potential danger. Because there is a heavy selective cost to being too curious, animal novelty seeking behavior is interlinked with neophobia (the avoidance of novelty), the very function that protects animals from engaging with uncertainty to avoid unsafe situations (Crane et al., 2020; Greenberg, 1990; Greenberg, 2003; Greggor et al., 2015). As such, a large part of the research using the novel stimulus paradigm in animals has focused on neophobia in relation to the social and ecological contexts, either suppressing or enhancing animals to become less or more neophobic (see reviews: Forss et al., 2017; Greggor et al., 2015; Mettke-Hofmann, 2014).

If an animal finds itself in an umwelt where the potential benefits of seeking information outweigh the risks, novel stimuli may instead trigger explorative and investigatory behaviors (Pisula, 2020). In this situation an animal can gain *additional information* regarding the physical properties of encountered stimulus, such as structure and weight, through physical exploration and manipulations. Thus, both cognitive predispositions and developmental demands combined with proximate and evolutionary environmental influences will influence a species exploration tendency and novelty-seeking behaviors (Mettke-Hofmann et al., 2002; Reber et al., 2021; Reader, 2015; Schuppli et al., 2017). Behavioral differences between generalist and specialist species towards novelty have been suggested to illustrate ecological reasons for variation (Bergman & Kitchen, 2009; Mettke-Hofmann et al., 2002; Tebbich et al., 2009). Generalist species feed on a broader dietary repertoire, which means young of such species also encounter more diverse habitats and food types already early in life. Thus, to learn and adaptively exploit a generalist diet, such species are likely predisposed to higher exploration tendencies, compared to narrow niche specialists (Greenberg, 1990; Greenberg, 2003). Although, this difference in exploration is not always true (Henke-von der Malsburg & Fichtel, 2018).

Various aspects of sociality have also been proposed to affect a species' intrinsic exploration tendency (i.e., the *Sozialwelt*). Exploration within a social unit can provide protection from danger by group members (Lehtonen & Jaatinen, 2016), but also generate competition for access to a potentially new resource (Greggor et al., 2016; Stöwe et al., 2006). One important aspect of social interactions is social learning. Social learning, spanning any learning process which is facilitated by observation or interaction with other animals (see review in Heyes, 1994), can facilitate an animal to explore its environment without experiencing the energy and fitness costs associated with individual exploration (Shier & Owings, 2007; van Schaik, 2010). Across generalist ape species, tested under similar captive environmental conditions, more solitary species showed higher innate exploration tendency and curiosity (Forss & Willems, 2022). Highly social species are rarely exploring alone and thus their predisposition to rely on social cues when and what to attend to is likely dependent on social facilitation or social learning of new food sources, compared to less social animals that frequently are dependent on individual exploration skills (Forss et al.,

2017). Moreover, highly social species arguably devote less time to exploring their environment as their intense social life requires sustained attention state towards conspecifics to monitor social interactions (Kano & Call, 2017; Laméris et al., 2022).

Both between and within species it is predicted that animals inhabiting safe environments can afford to be more explorative (Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001) than habitats that pose greater risk and increased danger. Captive animals are hypothesized to show greater explorative behaviors than wild conspecifics because of living in a risk-free environment (Barnett, 1958; Brown et al., 2013) or because they have more spare time and energy ("free time" and "excess energy" hypotheses) (Amici et al., 2020; Kummer & Goodall, 1985). Although systematic within species comparisons still are scarce, this "captivity effect" on novelty exploration has been reported in several species: rodents (Augustsson, & Meyerson, 2004; Pisula et al. 2012), hyenas (*Crocuta crocuta*) (Benson-Amram et al., 2013), various birds (Feenders et al., 2011; Rojas-Ferrer et al., 2020; Rössler et al. 2020) and primates (Forss et al., 2015, 2022). However, it remains unclear whether the captivity effect on explorative behaviors solely results from the absence of risk, or excess energy, or if it is also influenced by habituation towards humans and human-made objects. For example, orangutans that were more human-oriented were also more creative in their exploration, and in turn, better at solving problems (Damerius et al., 2017). Human habituation also increases exploration tendency in wild vervet monkeys (*Chlorocebus pygerythrus*) (Forss et al., 2022) and exposure to human facilities can improve their technical skills when faced with human provided tests (van de Waal & Bshary, 2010). These findings challenge the risk and excess energy hypothesis and instead suggest that human habituation may alter the risk-reward trade-off associated with novel stimuli that are often human-made and at the least, always presented by humans.

Here, we aim to systematically investigate how the properties of novel stimuli and the characteristics of individuals and their environments (umwelt) affect exploration behavior to investigate the proximate and ultimate causes of exploration and the origins of curiosity.

First, we examined the factors that affect exploration in wild meerkats (*Suricata suricatta*), a small, cooperatively breeding carnivore that inhabits the semiarid region of the Kalahari Desert. Our first aim was to evaluate the properties of novel stimuli that affect exploration. We tested whether meerkats recognize and regulate their behavior depending on if there is new information present by comparing behavioral responses between exposure to familiar versus unfamiliar stimuli with varying physical properties. To investigate how different properties of stimuli affect exploration, we designed a novel stimulus test battery containing multiple novel stimuli that varied in shape, color, smell, and edibility, and novelty.

Second, we were interested in how individual characteristics such as age, sex, or dominance affect exploration. Our test battery also allowed us to test for individual repeatability across different stimuli and over time. By doing so, we could test the hypothesis that variation in exploration behavior in meerkats meets the criterion for personality, which refers to any behavioral traits that are stable over time and context.

Third, because perception of risk may affect exploration and may vary depending on an animal's direct umwelt, we were also interested in addressing any potential effects on exploration caused by the presence of human observers and habituation levels during experimental data collection with wild meerkats. Next, we performed a within-species comparison using data from both captive and wild meerkats to further test for a potential captivity effect in exploration behavior between the two habitats.

Last, to investigate the role of the social environment on exploration, we also examined the effects of group size and social facilitation. In addition, we adapted a between species approach to examine exploration in wild meerkats and a closely related sympatric species, the yellow mongoose (*Cynictis penicillate*). While meerkats live in large, cooperatively breeding groups that consist of a dominant pair, adult subordinate helpers, and recent offspring, yellow mongooses live in small groups that consist of just a breeding pair and only their most recent offspring (Taylor & Meester, 1993). While both meerkats and yellow mongooses feed mainly on insects, yellow mongoose diet is more opportunistic and generalized (Bizani, 2014). Thus, the fourth aim of our study was to compare novelty response in the two mongoose species that live and evolved in the same environment, but with significantly different social lives and foraging strategies. Based on past studies of exploration tendencies between generalist and specialist

species, combined with the impacts a species social life is believed to have, we predicted that yellow mongooses would show higher curiosity and exploration towards novelty compared to meerkats.

Methods

Ethics Statement

This study was conducted with the permission of the ethical committee for animal research of the University of Pretoria (Permit Number: EC047-16 for meerkats and Permit Number: NAS210/2022 for the yellow mongooses) and the northern Cape Nature Conservation Service (FAUNA 1020-2016), South Africa. Ethical permit to conduct behavioral experiments on the captive population at the University of Zurich was obtained in accordance with Article 18 Animal Welfare Act from the Swiss Animal Welfare Ordinance, cantonal authorities: "Veterinäramt Zürich", Nr ZH185/2020.

Study Site and Species

In total, we tested 103 wild meerkats from six groups, 14 captive meerkats from one group, and five yellow mongooses from two groups. This resulted in a dataset of 732 observations (individuals x trials) for wild meerkats, 181 observations for captive meerkats, and 27 observations for wild yellow mongooses. Data on wild meerkats and yellow mongooses was collected between February and June 2021 at the Kalahari Research Center (henceforth KRC). The KRC is located in the Kuruman River Reserve in Northern South Africa (26°58'S, 21°49'E). Within the long-term Kalahari Meerkat Project (henceforth KMP), wild meerkat groups have been habituated to close human observations as well as occasional handling for weighing purposes. However, unhabituated meerkats sometimes join habituated study groups, and these individuals then undergo a protocol for habituation. During the time of this study (February 2021) not all individuals were fully habituated, and we therefore refer to these individuals as "partly habituated" in this article. For this study, we collected data on four fully "habituated" groups and two groups with both fully habituated and partly habituated" meerkats (Table 1).

During the time of this study there were no habituated yellow mongoose groups at the KRC and, in contrast to the meerkat groups, the yellow mongoose groups were not equipped with a radio collar or dye marked. Therefore, our sample size on yellow mongoose is reduced to only two unhabituated groups at the KRC (Table 1).

Data on captive meerkats were collected from October 2020 to January 2021 in the captive group of meerkats housed at the Animal Behavior Department at Irchel Campus at the University of Zurich, Switzerland.

Table 1

Meerkat and mongoose groups used for data collection

	Group Name	Group ID	Group Size Range (N)	# of unhabituated individuals
	Hakuna Matata	HM	17-19	0
Wild Fully	Namaqua	NQ	9-14	0
Habituated Groups	Runaways	RW	12-13	0
	Whiskers	W	14-19	0
Wild Partly	Gold Diggers	GD	15-26	4
Habituated Groups	Trackie-Daks	TD	12-17	4
Captive Meerkats	Irchel Big Group	Captive	13-14	NA
Wild Unhabituated	Gannavlakte	YMGV	2-4	4
Yellow Mongoose	Rus-en-Vrede	YMRV	2-4	4

Note. "Group Size Range" from beginning to end of data collection.

Experimental Procedure

We exposed the different wild mongoose groups to the same eight novel stimuli of which four items where potential novel foods (NF) – shrimp, mushrooms, raw minced meat, mozzarella – and four novel objects (NO) – red organic roses, plastic butterflies, cat toy mice with Baldrian herb scent, glass marbles – presenting a variety of materials and structures. The captive group of meerkats were exposed to exact same stimuli, except instead of raw shrimp, which were familiar to them, they received shell covered half-cooked tiger prawns. We also exposed both wild and captive meerkats to one familiar food item (wild groups: hardboiled egg, captive group: shell-free raw shrimp) and one familiar object (wild groups: porcupine spines, captive group: empty dye mark bowls) as control conditions. In both novelty and control conditions multiple items were presented to the meerkat groups to avoid any possible monopolization. The number of pieces depended on group size (approximately twice as many pieces as there were group members). For each group, the stimuli (including controls) were presented in a different order to avoid an order effect. Each group was tested once a week to avoid potential impact of seasonal variations and we performed an experiment with one category of novel stimuli per group per day, with minimum one week in between experimental sessions for each group.

Wild Meerkats

The burrow systems of wild meerkats consist of several openings that lead to underground tunnel systems connecting them to each other (Manser & Bell, 2004). It is common for meerkats to emerge from the same burrow entrance they went down the previous evening and to predict what burrow entrance the meerkats are most likely to emerge in the morning, the tested group was followed the evening before and the entrance where the last group member went down was marked with a drawn arrow into the sand. In the morning, we drew a square (around 12m^2) in front of the entrance the meerkats were most likely to emerge from (Figure 1a). We set up the experiments for the wild groups before sunrise, i.e., before the meerkats wake up and emerge from their sleeping burrow. To test for a potential influence of human presence caused by variation in habituation levels, half of the experiments per group were recorded with an observer (KB) present, while the other half were recorded with the human observer out of sight. For the experiments with human presence, three video cameras were used: two on tripods (Sony handycam HDR-FJ240E) covering all angles of the experimental grid, and one camera (Sony handycam HDRCX200) handheld by the human observer (KB). To keep the methods standardized, the duration of novelty exposure (i.e., total test time) was 20 min. For the experiments without human presence, only the two video cameras on tripods were used. In this case, we set everything up before sunrise, started the recordings and went out of sight. The observer then returned one hour after sunrise to make sure the total test time was at least 20 min.

Captive Meerkats

The captive meerkats were tested one hour after morning feeding routine in their indoor enclosure. Prior to testing, while the experimental setup was being installed, the whole group was moved to their outdoor enclosure (Figure 1b). Just like for the wild meerkats, a rectangular area was marked, and the behavioral responses were recorded from the moment a meerkat entered the rectangular area and the duration of novelty exposure (i.e., total test time) was 20 min. All experiments were video recorded from two different angles using a Xiaomi Action camera 4K to film the test session from above for individual recognition of the meerkats from their different dye marks, and one Sony handycam HDR-FJ240E from a side angle. All behavioral data were coded retrospectively from the videos.

Wild Yellow Mongoose

For the two yellow mongoose groups (YMGV and YMRV), the same novel stimuli and the control object were tested as for the wild meerkats. Just like meerkats, yellow mongooses live in burrow complexes,

which they often share with cape ground squirrels (*Geosciurus inauris*) or occasionally with meerkat groups. However, the yellow mongoose does not change its burrow system as frequently as the meerkats do. Despite not having gone through any active habituation process, the group living at GV farmhouse (26°96'S, 21°86'E) was relatively habituated to humans and did not show any behavioral reactions to human observers. Therefore, all experiments were conducted with an observer (KB) present. Because we were not able to locate the sleeping burrow of this group, we had to modify the experimental protocol. The YMGV group was usually seen around 10 am each day around the GV farmhouse. Therefore, we searched for them once a week around that time. Once found, several novel stimuli (of the same type) were presented a few meters from the group and their approach behavior was recorded with a Sony handycam by KD positioned a few meters away. The experiment lasted as long as the mongooses were in sight, but no longer than 20 min. The group living at Rus-en-Vrede (YMRV; 26°98'S, 21°84'E) was not habituated to human presence and therefore, observations with a human observer present were not possible. Instead, we used a motion-triggered video camera trap (Bushnell Core DS 30 MP, Model 119975C) to collect data on this group, a technique that has previously been reported useful to capture behavioural reactions to novel stimuli with unhabituated wild animals (Forss et al., 2022; Kalan et al., 2019). The camera trap was placed at an entrance to their burrow system. The same novelty categories were tested as in the YMGV group. Following the same protocol used for meerkats, the stimuli were placed in front of the burrow entrance. To maximize the probability of the mongooses encountering the presented novelty, both stimuli and camera trap were left in place for two days. Only five out of the nine categories of the 'test battery' were successful (rubber butterflies, cat toy mice, mushrooms, red roses, and shrimps), which reduced the number of data points this group of yellow mongooses could contribute to the analyses.

Figure 1

Illustrations of the set up for the novel stimuli presentations
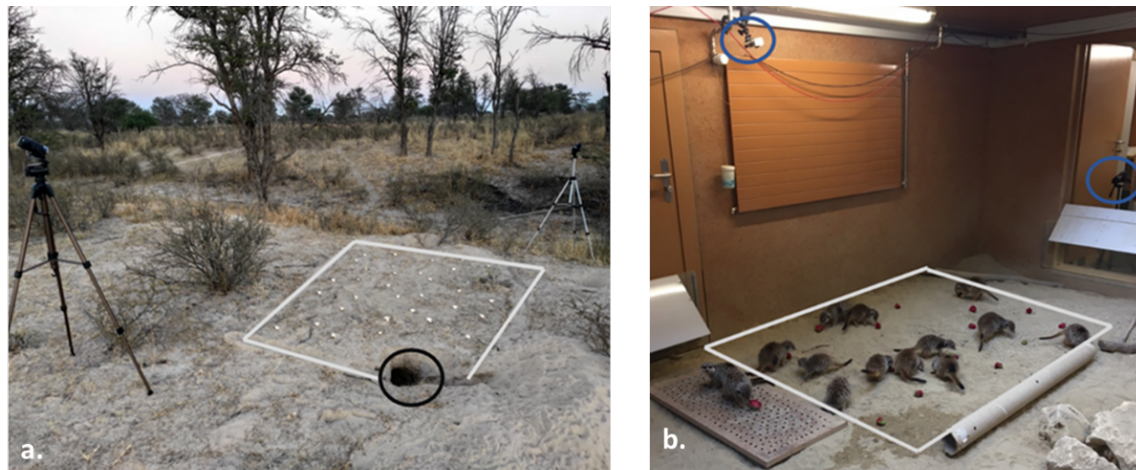
Note. 1a) Novel food (mozzarella balls) presented for the wild meerkats outside their overnight burrow hole. 1b) Novel objects (red roses) presented to the captive group of meerkats in their home enclosure.

Data Extraction

We analyzed all videos on the individual level using the software Mangold INTERACT (Mangold, 2020). This software allows the assessment of the reactions in slow-motion and direct coding of behaviors from the observed events on the videos. To avoid observational bias, an inter-observer test was performed. For this, 20% of the videos were also coded by a second, independent observer, who was not involved in the study and thus naïve to the behavioral expectations. The coded behaviors from the two independent observers were then compared and inter-observer reliability was calculated. The calculation revealed an "almost perfect" level of agreement (Cohen's Kappa κ = 0.82; McHugh, 2012). The

behavioral responses coded in Mangold INTERACT are listed in Table S1. The behavioral responses were categorized as state, event or calculated (formulas are indicated in the description of supplementary Table 1). State behaviors represent count data such as the number of sniffs, events represent continuous data where the time was measured in seconds, e.g., the duration of time spent in the experimental grid. Behavioral responses and predicted variables are described in Table 2.

Even though the different study groups differed in their total experimental time (5 min, 20 min, or 2 days), we ultimately chose not to control for these differences because experimental time did *not* correlate with amount of time an animal spent in the experimental grid. We also chose not to adjust exploration behaviors for time spent within the experimental grid. Time spent within the experimental grid varied widely, especially within wild meerkat groups (Figure S1). Time spent within the grid also appeared only weakly related to exploration behaviors, while individuals with high exploration scores do spend slightly more time in the experimental grid (Figure S2), other individuals spent large amounts of time in the grid because of sunning behavior (standing bipedally). Second, the reduced amount of time available to captive meerkats should, if anything, bias estimates of their exploration behavior down. However, our results show the opposite effect, captive meerkats spend slightly more time in the grid and were overall more explorative. Likewise, the yellow mongoose group (YMRV) that were exposed to stimuli over two days showed much lower levels of exploration and a reduced amount of time spent in the grid. Therefore, variation in experimental time does not appear to bias results. Furthermore, we were more interested in baseline explorative behaviors, rather than exploration rate, and controlling for time spent within the grid would have told us more about exploration rate, than the overall amount of exploratory behavior.

Table 2

List of variables used in statistical analyses

	Variables	Type	Description	Models
Response	Number of grid approaches	Count	The number of times a meerkat entered the experimental grid	M1.1, M2.1, M3.1, M4.1, M5.1
	Touch	Binary	Whether a meerkat touched a novel object at least once	M1.2, M2.2, M3.2, M4.2, M5.2
	Number of manipulations	Count	Number of times a meerkat manipulated a stimulus using the paws or mouth	M1.3, M2.3, M3.3, M4.3, M5.3
Predictors: Stimulus properties	Stimulus	Factor	Variable indicating the unique identity of each stimulus used	M1
	Stimulus novelty	Binary	Novel vs familiar	M2
	Stimulus type	Binary	Object vs food	M2-5
	Stimulus odor	Binary	Odor vs no odor	M2-5
Predictors: Individual traits	Age / Rank	Factor	Dominant, subordinate, or pup	M1-5
	Sex	Binary	Female vs male	M1-4
Predictors: Social factors	N present	Integer	Number of meerkats present during the trial	M1-5
	Pup presence	Binary	Whether pups were present during the trial	M1-3, M5
	Proportion of social approaches	Proportion	Proportion of approaches where at least one other meerkat was present in the grid	M1-5
	Group size	Integer	Number of meerkats in the group, regardless of how many were present during the trial	M1-5
Predictors: Habituation	Captivity	Binary	Captive vs wild	M4
	Human presence	Binary	Human present at trial or absent	M1-3, M5
	Habituation Level	Binary	Fully habituated from birth vs partly habituated	M1-3, M5
Other predictors:	Species	Binary	Meerkat vs yellow mongoose	M5
	Test order	Integer	Trial number to control for experience with the experimental grid	M1-5
	Weather	Binary	Sunny vs partly to fully cloudy	M1-3, M5

Note. Model numbers are abbreviated where all three sub-models are included (e.g., M1 is used as an abbreviation to indicate Models 1.1, 1.2, and 1.3 together).

Statistical Analyses

All statistical analyses were conducted in R (version 4.2.2; R Core Team, 2022) and RStudio (version 2022.07.1; RStudio Team, 2022). We used a series of generalized linear mixed models (GLMMs) to investigate our questions using the R package glmmTMB (Brooks et al., 2017). First, we created three models (M1.1-approach, M1.2-touch, M1.3-manipulate) to examine the possible effects of stimulus identity on our three response variables (Table 2) in the wild meerkat dataset (Figure S1). We included all relevant predictor variables, excluding those for captive meerkats or yellow mongooses and excluding those regarding stimulus properties because these were confounded with stimulus identity (Table S2). Next, we investigated whether wild meerkats distinguish novel from familiar stimuli by creating a second set of three models (M2.1-approach, M2.2-touch, M2.3-manipulate) that included stimulus novelty, stimulus type, and stimulus odor along with all relevant predictor variables (Table S3). Finally, to examine the factors affecting just novelty exploration we created three models (M3.1-approach, M3.2-touch, M3.3-manipulate) using the wild meerkat dataset with only novel stimuli and excluding familiar stimuli (Table S4). In models 3.1-3.3 we examine individual, social, habituation, and other factors (Table 2) alongside stimulus properties together to test our hypotheses regarding individual, social, and habituation effects. We also added interactions between sex and rank and between human presence and habituation *a priori.*

Because individual traits may also interact with social variables we also used the R package MuMIn for model exploration to identify important interactions between sex, rank, and all social variables (Bartoń, 2018). Only interactions included in over half of top models (delta <4) were retained in the final models (Table S5). Because model 3.3 (manipulate) showed a high intraclass correlation coefficient (ICC) for meerkat ID, we also used the R package rptR (Stoffel et al., 2017) to investigate the repeatability of individual performance across stimuli and over time.

We next created models to compare wild meerkats' behavioral responses to those of captive meerkats (M4.1-approach, M4.2-touch, M4.3-manipulate) and yellow mongooses (M5.1-approach, M5.2-touch, M5.3-manipulate). Overall, each response variable was used in five models each, though each of these models only differed by the inclusion or exclusion of just a few select variables to independently look at the effect of stimulus (M1), novelty (M2), factors affecting exploration (M3), captivity (M4), and species (M5).

Model fit was examined use the R package performance (Lüdecke et al., 2021) and DHARMa (Hartig, 2021). Marginal means were estimated using the R package emmeans (Lenth, 2022). Plots were produced using the R package ggplot2 (Wickham, 2016).

Results

Novel Information Recognition in Wild Meerkats

Our first analysis investigated whether wild meerkats respond differently to familiar versus novel stimuli. There were only a few behavioral differences between different stimulus types within the categories of food or object. First, meerkats were more likely to approach mushrooms than mozzarella and shrimp, and, second, meerkats were more likely to manipulate glass marbles compared to other novel objects (Table S3 and Figure S3)**.** Overall, meerkats were significantly less likely to approach both novel objects and novel food (β = -0.23*, p* = .01), but more likely to touch and manipulate novel objects than familiar objects (Touch Odds Ratio: 66.92 ± 40.52*, p* = < .001; Manipulate Odds Ratio: 8.95 ± 6.77*, p* = .004). Overall, the number of touches meerkats made towards novel objects was more similar to the number of touches made to food than familiar objects (Figure 2). Meerkats were also significantly less likely to manipulate novel food than familiar food (Manipulate Odds Ratio: 0.08 ± 0.02*, p* < .001; Figure 2 and Table S4).

Stimuli properties influencing exploration in wild meerkats

We next analyzed which stimuli properties influenced novelty exploration in Models 3.1-3.3. Whether a stimulus was an object or food or whether it had an odor did not influence the number of times meerkats approached the experimental grid (Food vs Object: β = -0.18, p = .07; Odor vs Odorless: β = -0.03, p = .85; Table S5; Figure 3). However, both stimulus type (object vs food) and odor affected the probability that a meerkat touched novel stimuli and the number of times meerkats manipulated novel stimuli (Touch Model: Food vs Object: β = 0.87, p = .01; Odor vs Odorless: β = -1.01, p = .04; Manipulate Model: Food vs Object: β = -0.77, p = .01, Odor vs Odorless: β = -1.65, p < .001). Overall, meerkats showed increased explorative behaviors towards odorless stimuli and meerkats were more likely to touch, but less likely to manipulate, novel food compared to novel objects.
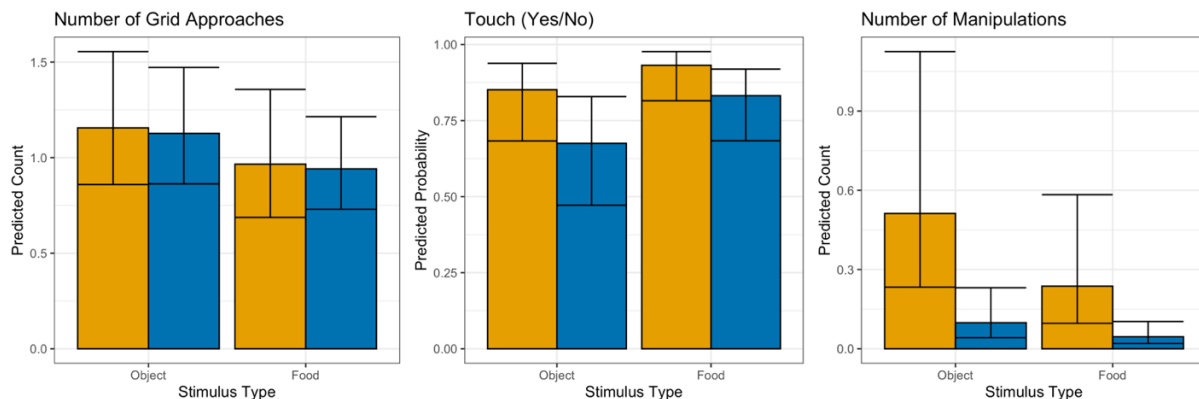
Figure 2

Behavioral responses to novel vs familiar objects and food in wild meerkats
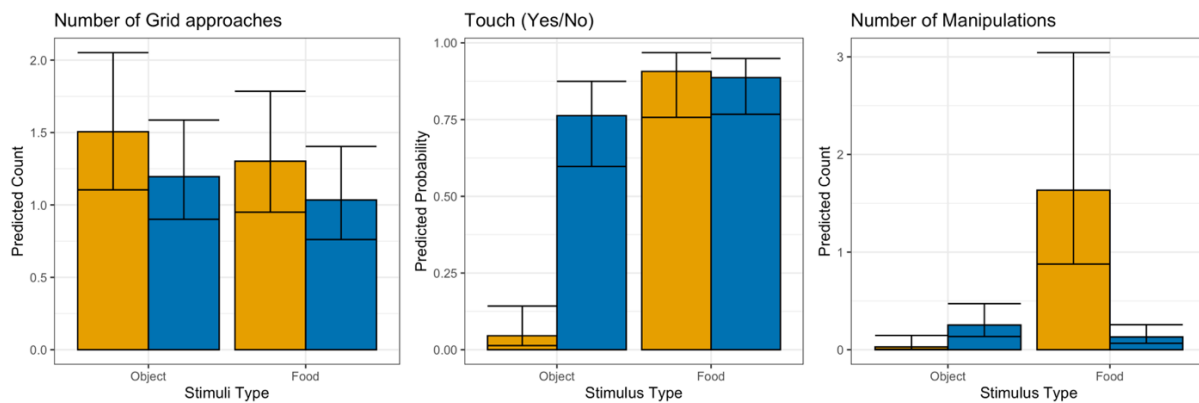
Note. Left: frequency of grid approaches, Middle: likelihood of touching stimuli (yes/no) and Right: frequency of physical manipulations. Familiar stimuli are in gold (light), novel stimuli are shown in blue (dark).

Figure 3

Exploration behavior towards novel objects versus novel food

Note. Stimuli with odor have blue fill (dark) and stimuli without odor have gold fill (light). Left: frequency of grid approaches, Middle: likelihood of touching stimuli (yes/no) and Right: frequency of physical manipulations.

## Individual Traits Influencing Exploration in Wild Meerkats

From the same models that we used to analyze stimulus properties (Table S5), we also investigated how individual traits, dominance-age class, and sex, affected exploration behaviors (Models 3.1-3.3). There were no direct effects of sex on the number of grid approaches or the likelihood of touching a novel stimulus, but male meerkats were more likely to manipulate novel stimulus compared to female meerkats ($\beta = 0.62$, $p = .03$). In addition, pups and subordinate meerkats were more likely to touch and manipulate novel stimulus compared to dominant meerkats (Touch model: subordinates: $\beta = 1.003$, $p = .02$; Manipulate model: pups: $\beta = 2.89$, $p = .002$, subordinates: $\beta = 2.29$, $p = .01$). Furthermore, the random effect of individual ID was very small for both the number of grid approaches and the probability of touching a novel stimulus. However, individual ID did explain some variation in the number of novel stimulus manipulations (Table S5). Therefore, we did an additional repeatability analysis on individual ID for the number of novel stimulus manipulations and found that individual ID explained a significant amount of variation after controlling for the effects of stimulus type and test order (Table S6: adjusted R = 0.28, $p = .003$, unadjusted R = 0.21, $p = .003$). However, individual ID was not significant after controlling for significant variables (odor/no-odor & Food/Object) from the Manipulate Model (Table S6).

Social Influences on Exploration in Wild Meerkats

We included four factors in our models related to social influences: the number of meerkats present, whether pups were present or not, the proportion of social vs solo grid approaches, and the overall size of the meerkat group (regardless of number present at a trial). The proportion of social approaches had a positive effect on the number of grid approaches ($\beta = 0.86$, $p < .001$). In addition, the presence of pups had a negative effect on the number of novel stimulus manipulations ($\beta = -0.84$, $p = .002$). Finally, the number of meerkats present had a positive effect on the number of grid approaches but negative effects on the likelihood of manipulating novel stimuli (Approach model: $\beta = 0.06$, $p < .001$; Manipulate model: $\beta = -0.07$, $p = .04$; Figure 4).

Figure 4

Exploration behavior in response to the presence of other meerkats
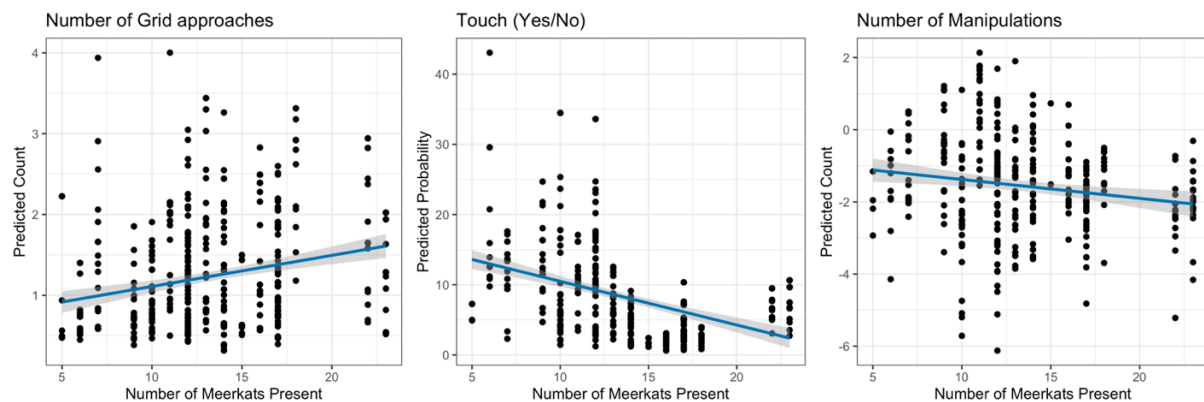
Note. Left: number of grid approaches, Middle: likelihood of touching (yes/no) novelty and Right: manipulation frequency in relation to the number of other meerkats present.

Human Influences on Exploration in Wild Meerkats

Finally, we investigated human influences on exploratory behavior in wild meerkats. We found a significant interaction between habituation level (fully vs partly) and the presence of a human observer on

both the number of grid approaches and the number of novel stimulus manipulations (Figure 5). In particular, partly habituated meerkats approached the grid more frequently when a human observer was present (Interaction: $\beta = 0.77$, $p < .001$), but had a much lower number of novel stimulus manipulations (Interaction: $\beta = -1.77$, $p < .001$).

Figure 5

Effect of human presence on wild meerkat exploration
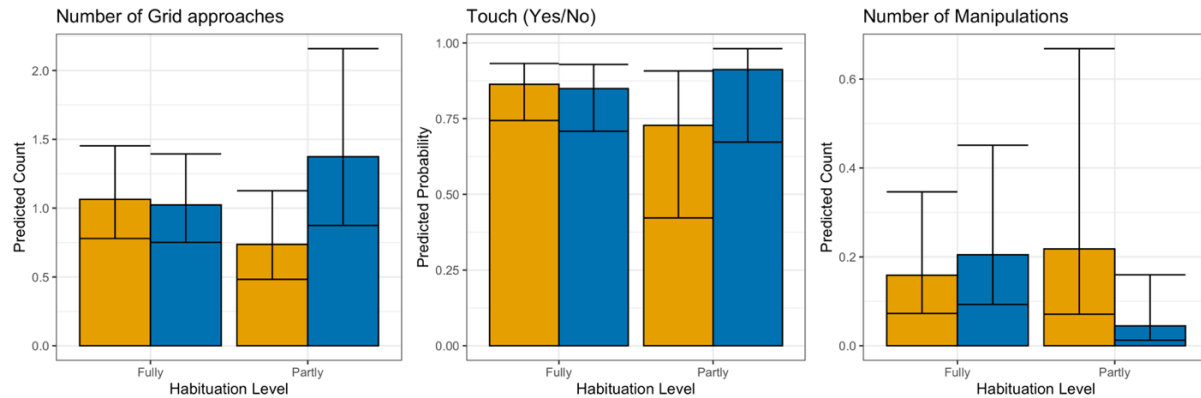
Note. Exploration behavior in response to absence of a human experimenter, visualized in gold fill (light) and the presence of human observer in blue fill (dark) in relation to individual habituation level. Left: frequency of grid approaches, Middle: likelihood of touching novelty (yes/no), and Right: manipulation frequency.

## Comparison Between Wild and Captive Meerkats

To test whether there is a "captivity effect" on novelty response in meerkats from two different habitats, captive and natural, we analyzed reactions to the same set of stimuli used for the wild meerkats (Models 4.1 – 4.3). Our models showed that wild meerkats were far less likely to approach, touch, and manipulate novel stimuli than captive meerkats (Figure 6; Table S7; Approach: $\beta = -3.98$, $p = .02$; Manipulate: $\beta = -12.68$, $p < .001$). Because 100% of captive meerkats touched all novel stimuli, we were not able to statistically compare the probability of touching novel stimuli. However, the raw percentage of wild meerkats touching novel stimulus was significantly less than 100% (Figure 6, middle). We also observed an interaction between habitat and the number of meerkats present, where the number of meerkats present had a positive effect on approaches and a negative effect on manipulation in wild meerkats, but in captive meerkats, the number of meerkats present had a negative effect on both approaches and manipulations (Approach Interaction: $\beta = 0.24$, $p = .05$; Manipulate Interaction: $\beta = 0.79$, $p = .002$).

Comparison Between Wild Meerkats and Wild Yellow Mongooses

In the final part of our analyses, we compared the behavioral responses between wild meerkats and wild yellow mongooses (Models 5.1 – 5.3; Table S8) and found that yellow mongooses were more likely to approach the experimental grid ($\beta = 2.70$, $p = .001$) and more likely to manipulate novel stimuli ($\beta = 1.75$, $p = .04$), but there was no difference in the probability of touching a novel stimulus (Figure 7).
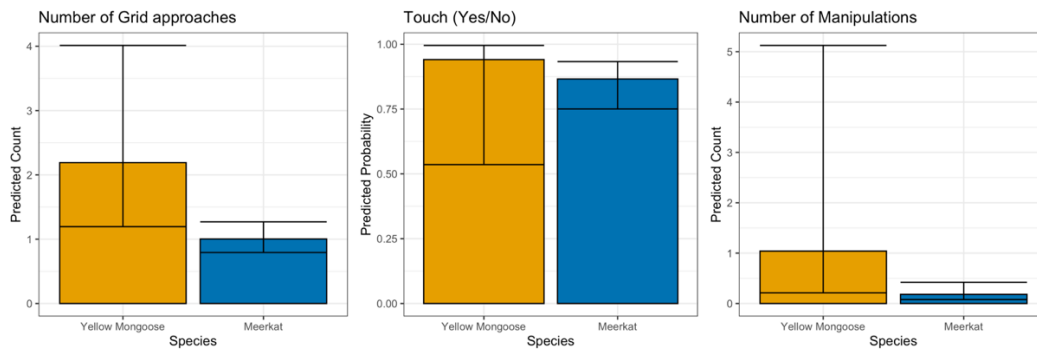
Figure 6

Exploration behavior in captive and wild meerkats
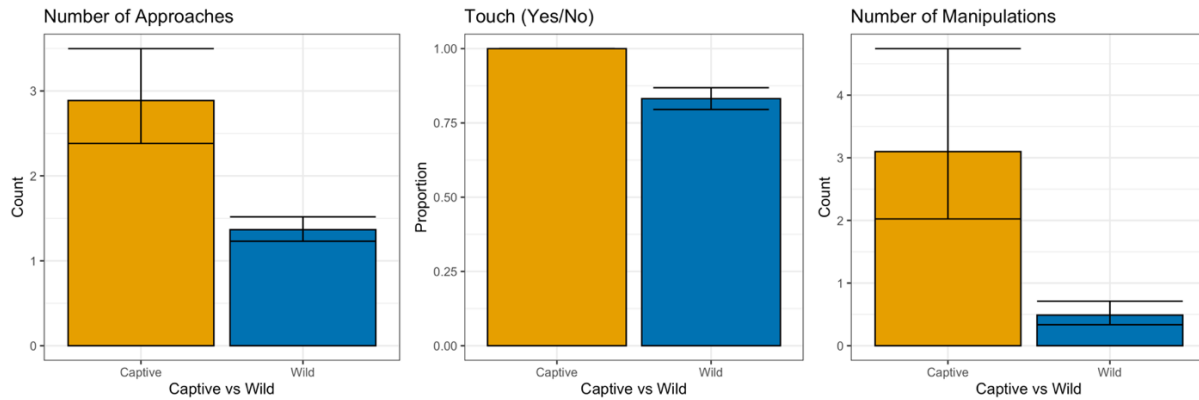
Note. Responses of captive meerkats shown in gold/light bars and wild meerkats in blue/dark bars. Left: Approach frequencies to the experimental grid, Middle: proportion of meerkats that touched novel stimuli (yes/no) and Right: manipulation frequencies of the novel stimuli.

Figure 7

Exploration behavior in wild yellow mongooses and wild meerkats

Note. Responses of wild yellow mongooses shown in gold/light bars and wild meerkats in blue/ dark bars. Left: Approach frequencies to the experimental grid, Middle: likelihood of touching novelty (yes/no) and Right: manipulation frequencies of the novel stimuli.

Discussion

We aimed to investigate how the properties of novel stimuli and the characteristics of individuals, and their environments (their umwelt), affected exploration behavior in captive and wild meerkats and wild yellow mongooses. We analyzed three levels of exploration behavior: number of approaches to the experimental grid, whether an individual touched a stimulus, and the number of stimulus manipulations. Overall, we found a significant influence of stimulus properties, individual traits, habituation levels, and social factors on novelty exploration.

When comparing familiar versus novel stimuli, wild meerkats were far less likely to touch familiar objects compared to novel objects and both novel and familiar food. These results suggest that meerkats are as interested in novel objects as they are in food. Thus, from the animal's perspective, it is possible that new food is examined in two steps: first, by assessing the novelty of an object, and only then by evaluating

it as a potential food itself. Accordingly, animals' response to novel food is like the reaction to a novel object in its initial stage. Furthermore, meerkats were also more likely to manipulate novel objects and familiar food compared to familiar objects and novel foods respectively, which supports previous research suggesting meerkats are food neophobic and that they generally manipulate a food item prior to eating it (Thornton, 2008). Interestingly, the increase in the number of manipulations towards novel objects was largely driven by manipulation of glass marbles. This result suggests that it may not be the novelty of the stimulus per se that increased manipulation behavior, but some other property of the glass marbles, which were the only smooth and shiny novel object in the test battery. However, when taken together, these results suggest that meerkats likely can distinguish novel stimuli from familiar stimuli and adjust their exploration behaviors accordingly. As such our findings support the idea that exploration behavior is a way of information seeking in animals (Rojas-Ferrer et al., 2020; Pisula, 2020).

We next investigated the factors that correlated with variation in response to just novel stimuli in wild meerkats. We found that odor had a significant negative effect on the likelihood of a meerkat touching a novel stimulus and on the number of manipulations directed towards novel stimulus. In other words, non-smelly items triggered greater exploration. Meerkats are highly reliant on their olfactory sense to gather information in their environment (Manser, 2018 for review) and this result suggests that when a stimulus failed to emit any olfactory information, meerkats likely sought more information about that stimulus via physical touch and manipulation. Meerkats were also more likely to touch novel foods but less likely to manipulate them compared to novel objects which again corresponds with a general aversion towards consuming novel foods (Thornton, 2008).

Dominant meerkats were much less likely to touch or manipulate novel stimulus compared to subordinates and pups, and female meerkats were less likely to manipulate novel stimulus compared to males. Subordinate and juvenile male meerkats have also been shown to be more likely to solve innovative problem-solving tasks than older adults and dominants (Samson & Thornton, 2012). Thus, in accordance with previous findings, our results suggest that this distinction between age-sex classes is apparent also in underlying explorative behaviors. Although, this is a finding that seems to generalize to other animal species as well (overview in: Sherratt & Morand-Ferron, 2018), it is not always the case as some research suggests that adults are more likely to innovate (Reader & Laland, 2001), and for example in callitrichid monkeys tested in captivity competitiveness had an influence on object exploration with dominant individuals securing access (Kendal et al., 2005). In our view, such contradictory findings highlight the importance of considering the role of the tested animal's umwelt, and the expected variation between captive and wild individuals due to the captivity effect. Moreover, in meerkats, dominant individuals may have less time to dedicate to exploration due to their social role within the group, whereas younger individuals, which experience less demand to monitor or assert dominance over other group members, may have more time to dedicate to exploration, aligning with the "free time hypothesis" on an intraspecific level (Amici et al. 2019). As the dispersing sex, information gathering may be more important for male meerkats and thus their intrinsic motivation to explore may be higher. Furthermore, while there was very little individual variation in approach and touching novel stimuli, there was some weak, but significant repeatability of manipulation behavior within individual meerkats. This suggests that exploration requiring physical manipulation may be a personality trait in meerkats because manipulation behavior was measured both across a wide array of stimuli and over time. Repeatability over time and context are the two requirements for a behavioral trait to be considered personality (see reviews: Cabrera et al., 2021; Carter et al., 2013; Sih et al., 2015).

We also found some evidence for social facilitation of exploration behavior in wild meerkats. The number of meerkats present, and the proportion of social approaches, correlated with increased approaches towards the experimental grid. This suggests that meerkats may have approached the grid in part due to the presence of another meerkat rather than seeking information about novel stimuli, especially because the number of meerkats present, and proportion of social approaches, did not increase the likelihood that a meerkat touched or manipulated a novel stimulus, i.e., the presence of social partners within the grid reduced neophobia in approaching novel stimulus but did not increase physical exploration of it. In addition, both the number of meerkats present, and the presence of pups, were associated with decreased

manipulative exploration behavior which suggests a potential role of social interference on exploration. This may be particularly true for species with high sociality as both time and cognitive load will be dedicated to species typical social behaviors. Such impact of sociality can potentially go two ways: it can increase exploration in some individuals whilst other conspecifics are present for vigilance (Dukas, 2009) or it can decrease exploration due to social inhibition or interference (Griffin et al. 2013; Kerman et al. 2018). Here, we suspect decreased exploration in the presence of pups may be a result of altered attentional demands, as the focus of attention may be on monitoring offspring rather than exploration.

We were next interested in how human habituation and the presence of a human observer during experiments affected exploration behavior in wild meerkats to test hypotheses about the "captivity effect" where captive animals typically show greater exploration than wild animals (Forss et al., 2015). Interestingly, our data showed that fully habituated groups did not show any significant differences in exploration behavior when a human observer was present versus absent, which suggests that they largely ignore human presence and behave as if a human was part of the environment. However, partly habituated meerkats, that had not undergone habituation as pups and thus were only partially accustomed to human observers, were more likely to approach the experimental grid when a human was present, yet human presence made them less likely to manipulate novel stimuli. This puzzling result could imply that during the habituation process meerkats associate humans with both risk and reward (food is regularly used during weighing sessions). Approaching the grid is a relatively low-risk behavior and may correspond with an expectation of a food reward. However, further exploration and manipulation of stimulus is relatively higher risk and partly habituated meerkats may be reluctant to remain near the human observer for a longer period in order to undertake riskier exploration behaviors. As expected, we also found that captive meerkats were more explorative across all behaviors. While our data cannot necessarily partition when exploration behavior results from free time, risk, and habituation, the results from the human presence effect in wild meerkats combined with the captive-wild comparison suggest that human habituation likely plays a role in altering the risk-reward response towards novel (human-made) stimulus. Balancing risk-reward tradeoffs caused by humans or indirect human presence has also been suggested as an important underlying mechanism of how animals habituate and adapt to urban environments (Uchida et al. 2019). Like our findings, captivity and human habituation have also reportedly increased exploration in other species (Benson-Amram et al., 2013; Forss et al., 2022; Fox & Millam, 2004), yet to what extent this pattern has roots in animals' changed perception of humans and their artefacts or ecological variables related to food availability and time budgets remains to be disentangled. However, the hypothesis that altered behavior in captive animals or in animals experiencing urbanization is largely a result of habituation and reduced reactivity to humans or human artefacts has intriguing (or alarming) parallels to process of domestication (e.g., Harveson et al., 2007). The 'self-domestication' hypothesis suggests that selection against reactivity towards humans alone is sufficient to result the suite of phenotypic changes seen in domesticated species (Hare et al., 2005).

When we compared wild meerkats to wild yellow mongooses, we found that yellow mongooses were more likely to approach the experimental grid and we also found some evidence that yellow mongooses were more likely to manipulate novel stimuli. Because yellow mongooses are less social than meerkats, they may depend more on learning about their environment through individual exploration compared to meerkats. In addition, yellow mongooses feed more on prey items on the surface of the sand, rather than buried prey items, and as a result they may be more prone to explore novel items on the surface of the sand compared to meerkats which mainly dig for prey items.

Conclusions

We showed that wild mongoose can and do perceive differences between novel and familiar stimuli, an important validation of the novel stimulus paradigm. However, we also found that stimuli properties such as odor, object versus food, and the unique properties of glass marbles all affected exploration responses. We also found differences in exploration behavior based on the exploration metric

that we analyzed; approaching novel stimulus likely only requires or uses visual information, while touching may use both visual and olfactory information, and manipulation allows subjects to gather physical information in much greater detail. Very few factors affected approach behavior, but we did find significant influences of our predictor variables on the likelihood of touching and manipulation stimuli. Overall, these findings generate the recommendation that a species capacities and natural behaviors should be considered when choosing stimulus used during novel object or novel food presentations and when choosing appropriate metrics of exploration behavior.

Overall, our multi-level approach demonstrates how the Sozialwelt (social world), Merkwelt (perceptual world), and possibly the Wirkwelt (motor world), together can influence behavioral responses to novel stimulus in meerkats and mongooses. We show that meerkats likely use multiple senses when gathering information about something novel, including visual, touch, and olfactory cues and that the kinds of cues emitted by novel stimulus thus affect their exploration behavior. Our findings generally add to the literature suggesting that exploration behavior may vary among individuals based on age, sex, habituation, and individual personality and is also influenced by social context and species ecology (Forss et al., 2017; Greggor et al. 2015; Mettke-Hofmann, 2014).

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Author Contributions: KB: collected the data, preliminary statistical analyses, writing of manuscript and performed the study within the scope of her MSc thesis, LJU: statistical analyses and writing of the manuscript, JS: coded behavioral data from the videos, SF: conceptualization of the study, acquired funding, designing experiments, and writing of the manuscript.

Data Accessibility: The data that support the findings of this study are available on request from the corresponding author.

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Supplementary Materials

Table S1

Behavioral responses coded from the videos of the experiments

Parameter	Levels	Level names	Description
Present	2	0	Individual was not present during experiment
		1	Individual was present during experiment
Approached	2	0	Individual did not approach the experimental grid
		1	Individual did approach the experimental grid
Eat food	2	0	Individual did not eat the presented food item
		1	Individual ate the presented food item
Approach type	2	Individual	Individual entered experimental grid when no conspecific was inside the grid
		Social	Individual entered the experimental grid when another conspecific already was inside the grid
Behavioral response	**Type**		**Description**
Nr. social approaches	Calculated		Sum of an individual's social approaches
Nr. individual approaches	Calculated		Sum of an individual's individual approaches
Nr. grid approaches	Calculated		Nr. social approaches + Nr. individual approaches
Nr. sniffs	State		+1 every time the individual sniffed at the presented item
Nr. manipulation events	State		+ 1 every time the individual touched or manipulated (using paws or mouth) the presented item
Nr. exploration events	Calculated		Nr. Sniffs + Nr. Manipulation events
Manipulation duration [s]	Event		The total duration the individual spent manipulating the presented item per experiment in seconds
Latency to interact [s]	Event		Time in seconds the individual needed to interact with the presented item after entering the experimental grid
Time in grid [s]	Event		The total time the individual spent inside the experimental grid in seconds
Total test time [s]	Event		Time in seconds from start until end of experiment (max. 1200)
Time in grid percentage [%]	Calculated		Time in grid [s]/ Total test time [s] * 100
Ratio of social approaches	Calculated		Nr. social approaches/ Nr. grid approaches
Exploration rate [1/min]	Calculated		Nr. exploration events/ Total test time/ 60

Figure S1

Between group variation in the amount of time spent in the experimental grid with and without a human present
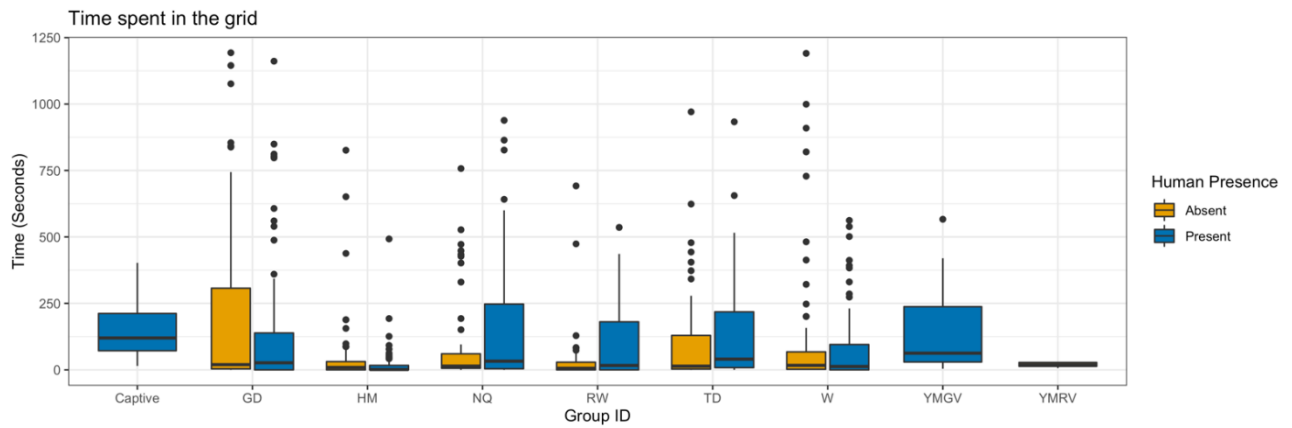
Note. "Captive" represents the captive meerkat group. All two-character IDs are wild meerkats. Group IDs starting with "YM" are wild yellow mongoose groups.

Table S2

Variation in the amount of time spent in the experimental grid

ANOVA		Df	F	P
	Species x Status	2	3.14	**.04**
		Estimate	SE	P
Pairwise Contrasts	Captive Meerkats vs Wild Meerkats	34.9	16.0	.06
	Captive Meerkats vs Yellow Mongoose	124.0	87.1	.33
	Wild Meerkats vs Yellow Mongoose	88.1	86.2	.56

Figure S2

Relationship between the amount of time spent in the experimental grid and the number of stimulus manipulations
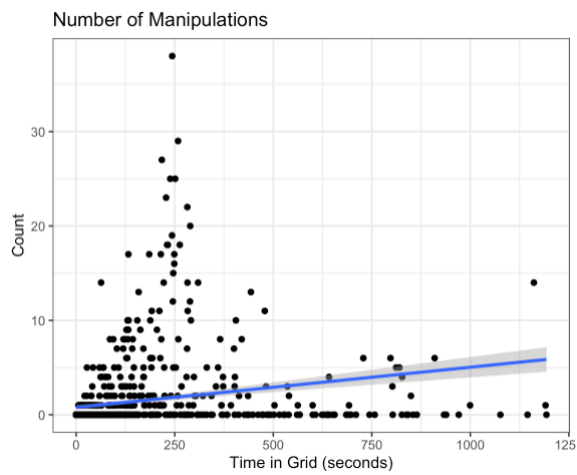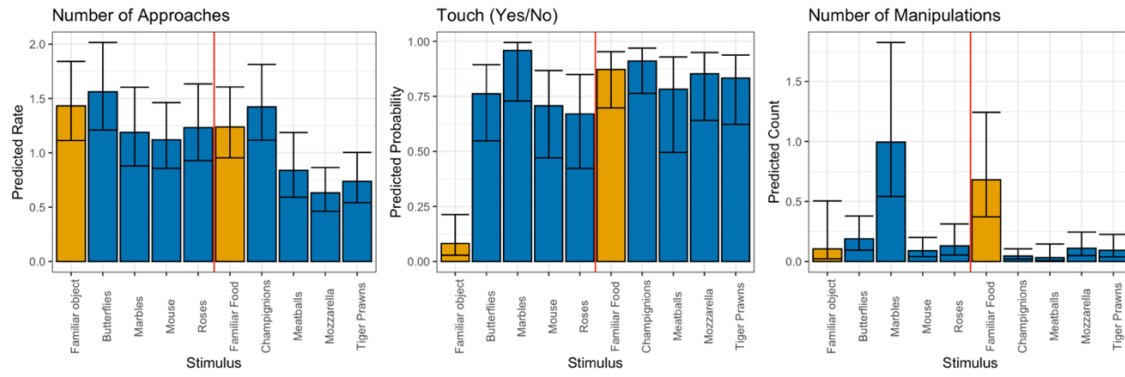
Figure S3

Behavioral responses to different stimuli in wild meerkats

Note. Familiar stimuli are in gold, novel are shown in blue. The vertical red line indicates a separation between objects and food.

Table S3

Pairwise contrasts examining behavioral responses to different stimuli in wild meerkats

	Approach Model (M1.1)			Touch Model (M1.2)			Manipulate Model - (M1.3)		
Model Type	Poisson (link=logit)			Binomial (link=log)			Poisson (link=logit)		
N Observations	731			529			398		
N Subjects	102			100			99		
N Groups	6			6			6		
	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Familiar object - Butterflies	-0.09	0.15	1.00	-3.59	0.64	**<.0001**	-0.60	0.81	1.00
Familiar object - Marbles	0.19	0.15	.97	-5.57	1.12	**<.0001**	-2.26	0.76	.09
Familiar object - Mouse	0.25	0.14	.74	-3.30	0.55	**<.0001**	0.15	0.80	1.00
Familiar object - Roses	0.15	0.15	.99	-3.13	0.59	**<.0001**	-0.22	0.83	1.00
Butterflies - Marbles	0.27	0.16	.81	-1.99	1.12	.75	-1.66	0.31	**<.0001**
Butterflies - Mouse	0.33	0.15	.43	0.28	0.57	1.00	0.74	0.38	.62
Butterflies - Roses	0.24	0.16	.88	0.45	0.53	1.00	0.38	0.40	1.00
Marbles - Mouse	0.06	0.16	1.00	2.27	1.10	.56	2.40	0.34	**<.0001**
Marbles - Roses	-0.04	0.17	1.00	2.44	1.12	.47	2.03	0.41	**<.0001**
Mouse - Roses	-0.10	0.16	1.00	0.17	0.54	1.00	-0.37	0.46	1.00
Familiar Food - Mushrooms	-0.14	0.13	.99	-0.40	0.62	1.00	2.71	0.33	**<.0001**
Familiar Food - Meatballs	0.39	0.18	.48	0.64	0.66	.99	3.06	0.74	**.002**
Familiar Food - Mozzarella	0.67	0.16	**.00**	0.17	0.62	1.00	1.83	0.29	**<.0001**
Familiar Food - Tiger Prawns	0.52	0.17	**.07**	0.31	0.65	1.00	1.99	0.39	**<.0001**
Mushrooms- Meatballs	0.53	0.18	.10	1.04	0.71	.91	0.36	0.79	1.00
Mushrooms- Mozzarella	0.81	0.15	**<.001**	0.57	0.64	1.00	-0.88	0.37	.35
Mushrooms- Tiger Prawns	0.66	0.16	**.001**	0.71	0.64	.98	-0.72	0.45	.84
Meatballs - Mozzarella	0.28	0.20	.91	-0.48	0.68	1.00	-1.24	0.77	.84
Meatballs - Tiger Prawns	0.13	0.21	1.00	-0.33	0.75	1.00	-1.07	0.81	.95
Mozzarella - Tiger Prawns	-0.15	0.19	1.00	0.15	0.68	1.00	0.16	0.45	1.00

Table S4

Behavioral responses to novel vs familiar objects and food in wild meerkats

	Approach Model (M2.1)			Touch Model (M2.2)			Manipulate Model (M2.3)		
Model type	Poisson (link=logit)			Binomial (link=log)			Poisson (link=logit)		
N observations	731			529			398		
N subjects	102			100			99		
N Groups	6			6			6		
	Estimate	SE	*p*	Estimate	SE	*p*	Estimate	SE	*p*
Object vs Food	-0.15	0.09	.12	4.21	0.61	**<.001**	2.16	0.76	**.004**
Novel vs Familiar	-0.23	0.08	**.01**	5.32	0.80	**<.001**	4.02	0.79	**<.001**
Novel * Object	-	-	-	-4.43	0.82	**<.001**	-4.68	0.80	**<.001**
Odor vs Odorless	0.03	0.11	.80	-0.91	0.49	.06	-1.72	0.28	**<.001**
Dominant vs pup	0.22	0.14	.11	0.24	0.46	.60	1.59	0.61	**.01**
Dominant vs subordinate	0.15	0.12	.19	0.90	0.39	**.02**	1.50	0.59	**.01**
Female vs Male	-0.05	0.07	.46	-0.33	0.26	.20	0.50	0.27	.06
N Present	0.06	0.02	**<.001**	-0.07	0.05	.16	-0.01	0.03	.61
Pups Present (Yes/No)	0.14	0.09	.10	0.09	0.32	.78	-0.35	0.21	.09
Proportion Social	0.73	0.08	**<.001**	0.44	0.32	.17	0.44	0.18	**.02**
Human Present (Yes/No)	-0.13	0.08	.10	-0.11	0.29	.71	0.30	0.16	.06
Habituated (Yes/No)	-0.46	0.16	**.004**	-0.07	0.48	.88	-0.55	0.36	.13
Human x Habituation	0.73	0.17	**<.001**	-	-	-	-	-	-
Test Order	-0.06	0.02	**<.001**	0.01	0.06	.82	0.06	0.05	.24
Weather - Sunny	0.00	0.08	.98	-0.44	0.35	.21	-0.72	0.20	**<.001**
ICC (Subject)	0.002			0.000			0.460		
ICC (Group)	0.126			0.098			0.000		
Pairwise Contrasts									
	Odds Ratio	SE	*P*	Odds Ratio	SE	*P*	Odds Ratio	SE	*P*
Novel Object vs Familiar Object	-	-	-	67.33	41.05	**<.001**	8.64	6.54	**.005**
Novel Food vs Familiar Food	-	-	-	0.80	0.39	.66	0.08	0.02	**<.001**

Table S5

Behavioral responses to novel stimuli in wild meerkats

	Approach Model (M3.1)			Touch Model (M3.2)			Manipulate Model (M3.3)		
Model type	Poisson (link=logit)			Binomial (link=log)			Poisson (link=logit)		
N observations	579			404			336		
N subjects	101			100			98		
N Groups	6			6			6		
	Estimate	**SE**	***p***	**Estimate**	**SE**	***p***	**Estimate**	**SE**	***p***
Food vs Object	-0.18	0.10	.07	0.87	0.35	**.01**	-0.77	0.29	**.01**
Odor vs Odorless	-0.03	0.13	.85	-1.01	0.50	**.04**	-1.65	0.30	**<.001**
Dominant vs pup	0.30	0.16	.06	0.69	0.50	.17	2.89	0.92	**.002**
Dominant vs subordinate	0.17	0.14	.21	1.00	0.42	**.02**	2.29	0.89	**.01**
Female vs Male	-0.04	0.08	.59	-0.35	0.29	.22	0.62	0.29	**.03**
N Present	0.06	0.02	**<.001**	-0.07	0.05	.19	-0.07	0.03	**.04**
Pups Present (Yes/No)	0.18	0.10	.06	-0.04	0.34	.92	-0.84	0.27	**.002**
Proportion Social	0.86	0.09	**<.001**	0.38	0.35	.28	0.21	0.22	.35
Human Present (Yes/No)	-0.06	0.09	.54	0.09	0.33	.78	0.23	0.20	.24
Habituated (Yes/No)	-0.45	0.18	**.01**	-0.10	0.53	.86	0.17	0.43	.70
Human x Habituation	0.77	0.20	**<.001**	-	-	-	-1.77	0.46	**<.001**
Test Order	-0.06	0.02	**<.001**	0.03	0.07	.68	0.11	0.05	**.05**
Cloudy vs Sunny	-0.06	0.10	.57	-0.46	0.39	.24	-0.56	0.23	**.01**
ICC (Subject)	0.000			0.000			0.397		
ICC (Group)	0.07			0.086			0.000		
	Pairwise Contrasts								
	Odds Ratio	SE	*p*	Odds Ratio	SE	*p*	Odds Ratio	SE	*p*
Human Present: Partly vs Fully Habituated	1.37	0.26	.09	-	-	-	0.20	0.10	**.001**
Human Absent: Partly vs Fully Habituated	0.64	0.11	**.01**	-	-	-	1.18	0.51	.70
Partly Habituated: Human Present vs Absent	2.04	0.36	**<.001**	-	-	-	0.22	0.09	**<.001**
Fully Habituated: Human Present vs Absent	0.95	0.09	.54	-	-	-	1.26	0.25	.24

Table S6

Results from repeatability analysis for subject ID on the number of manipulations

Model Type	R	SE	N	CI	P
Adjusted R while controlling for stimulus type and test order	0.279	0.126	98	0.003,0.472	.003
Unadjusted R while controlling for stimulus type and test order	0.210	0.094	98	0.003,0.347	.003
Adjusted R while controlling for all significant variables from M3.3	0.131	0.125	98	0,0.325	.102
Unadjusted R while controlling for all significant variables from M3.3	0.106	0.078	98	0.011,0.249	.095

Table S7

Behavioral responses to novel stimuli in captive versus wild meerkats

|	Approach Model (M4.1)			Enter Model – Yes/No (M4.2)			Manipulate Model (M4.3)		
Model type	Generalized Poisson (link=log)			Binomial (link=log)			Generalized Poisson (link=log)		
N observations	731			556			578		
N subjects	115			116			113		
	Estimate	SE	*p*	Estimate	SE	*p*	Estimate	SE	*p*
Object vs Food	-0.06	0.09	.48	NA	NA	NA	-0.89	0.19	**<.001**
Odor vs Odorless	-0.15	0.10	.14	NA	NA	NA	0.86	0.19	**<.001**
Dominant vs pup	0.28	0.12	**.02**	NA	NA	NA	1.08	0.36	**.002**
Dominant vs subordinate	0.00	0.09	.99	NA	NA	NA	0.56	0.27	**.04**
Female vs Male	-0.04	0.06	.53	NA	NA	NA	0.29	0.15	.06
N Present	-0.23	0.12	**.05**	NA	NA	NA	-0.81	0.25	**.001**
Proportion Social	0.91	0.09	**<.001**	NA	NA	NA	0.80	0.26	**<.001**
Wild vs Captive	-3.98	1.66	**.02**	NA	NA	NA	-12.68	3.55	**<.001**
Captivity x N Present	0.24	0.12	**.05**				0.79	0.25	**.002**
Test Order	0.01	0.01	.36	NA	NA	NA	-0.14	0.03	**<.001**
ICC (Subject)	0.000			NA			0.029		

Table S8

Behavioral responses to novel stimuli in wild meerkats versus yellow mongooses

	Approach Model (M5.1)			Touch Model (M5.2)			Manipulate Model – Count (M5.3)		
Model type	Poisson (link=logit)			Binomial (link=log)			Poisson (link=logit)		
N observations	605			429			360		
N subjects	107			105			103		
N Groups	8			8			8		
	Estimate	**SE**	*p*	**Estimate**	**SE**	*p*	**Estimate**	**SE**	*p*
Food vs Object	-0.01	0.25	.97	1.00	0.35	**.004**	0.04	0.25	.89
Odor vs Odorless	-1.76	0.26	**<.001**	-1.05	0.49	**.03**	-1.74	0.25	**<.001**
Dominant vs pup	2.91	0.90	**.001**	0.65	0.50	.20	2.88	0.92	**.002**
Dominant vs subordinate	2.34	0.87	**.01**	1.01	0.41	**.01**	2.34	0.89	**.01**
N Present	-0.08	0.04	**.02**	-0.04	0.06	.51	-0.07	0.04	.06
Pups Present (Yes/No)	-0.67	0.26	**.01**	0.04	0.34	.90	-0.59	0.26	**.03**
Proportion Social	0.06	0.20	.76	0.40	0.35	.25	0.10	0.20	.61
Human Present (Yes/No)	0.11	0.20	.59	-0.05	0.35	.88	0.07	0.20	.72
Habituated (Yes/No)	0.18	0.49	.71	-0.54	0.57	.35	0.01	0.53	.99
Human x Habituation	-1.73	0.46	**<.001**	1.55	0.82	.06	-1.39	0.44	**.001**
Yellow Mongoose vs Meerkat	2.70	0.83	**.001**	0.90	1.40	.52	1.75	0.85	**.04**
Test Order	0.09	0.04	**.03**	0.03	0.07	.65	0.09	0.04	.05
Cloudy vs Sunny	0.17	0.17	.32	-0.24	0.38	.53	0.23	0.17	.19
ICC (Subject)	0.000			0.000			0.396		
ICC (Group)	0.068			0.090			0.101		

Figure S4

Group differences in exploration behavior by species
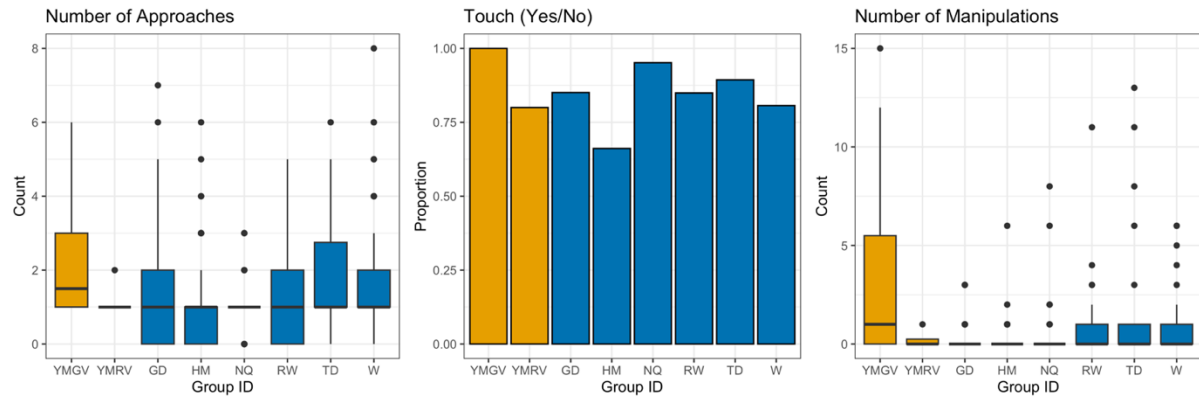
Note. Light yellow = yellow mongoose; dark blue = meerkats.