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RESEARCH ARTICLE

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Can you dig it? The impact of a movable substrate "dig pit" on naked mole rat (*Heterocephalus glaber*) behavior and welfare

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Abstract

Zoos are often limited by exhibit design in the opportunities they can provide animals to express natural behaviors; however, the opportunity to perform certain natural behaviors is key to supporting good animal welfare. Traditionally, in zoos, naked mole rats (*Heterocephalus glaber*) are housed in gunite-lined acrylic chambers that replicate the look of their tunnel systems in the wild but don't offer the opportunity for natural digging and tunnel construction behaviors. In this study, naked mole rat behavior was evaluated when providing two different presentations of movable substrate added on to the original exhibit—a tank with loose substrate and a dig pit with hard-packed clay. We recorded 299 5-min focal observations with 30-s intervals and 30 group scans to understand behavioral changes across treatments (10 days of observation per treatment). Results were analyzed using Bayesian mixed models. Digging behavior emerged in both presentations of moveable substrate. A potential indicator of negative welfare, barrier-directed behavior, decreased when the mole rats had access to the tank of loose substrate. A potential indicator of positive welfare, exploratory behavior, increased with access to the dig pit when the mole rats had the opportunity to build tunnels. Additionally, affiliative social interactions increased, and aggressive interactions decreased with access to either presentation of movable substrate. The observed changes in colony behavior demonstrate that captive naked mole rats readily exhibited the natural behaviors of digging and tunnel building when the opportunity was presented, and the habitat modification likely improved naked mole rat welfare.

KEYWORDS

animal welfare, exhibit design, natural behaviors

1 | INTRODUCTION

While there are many definitions of animal welfare, nearly all acknowledge that the opportunity to express certain natural behaviors is essential (reviewed in Veasey, 2017; Veasey et al., 1996; Fraser, 2008, see also Mellor & Beausoleil, 2015). In general, the opportunity to express behaviors associated with a strong motivation will support good animal welfare (Browning, 2020). Even if the expression of a natural behavior itself does not necessarily indicate good welfare across all welfare frameworks, most agree that frustration caused by the inability to fulfill an evolved motivation to perform some natural behaviors can compromise welfare (Cronin & Ross, 2020; Veasey et al., 1996, 2017). Related, the time void created by removing a part of the species-typical activity budget can also impair welfare (Veasey, 2017). As such, while the exact relationship between natural behaviors and welfare states isn't agreed upon, it is clear that providing opportunities to express highly motivated, natural behaviors is likely to support good animal welfare and may even be related to positive affective states with beneficial, long-term impacts (Špinka, 2006).

Habitat design in zoos often dictates what opportunities are available (or can be made available) to animals to express natural behaviors. For example, in tiger (*Panthera tigris*) exhibits designed to resemble the networks of "special use" areas that make up their territories in the wild, tigers were more active, showed more exploratory behaviors and expressed less stereotypical behaviors (Smith et al., 2023). In another study, tamarins (*Saguinus imperator subgrisescens*, *Sauinus bicolor*) in free-ranging, naturalistic exhibits locomoted more and showed some vocalizations more than tamarins living in caged housing (Bryan et al., 2017). Additionally, some research paradigms have demonstrated the high value animals place on expressing natural behaviors. For example, domestic chickens (*Gallus gallus domesticus*) have a natural motivation to perch at night and pushed open significantly heavier doors to gain access to a nighttime perching option than a door without that option (Olsson & Keeling, 2002). In another example, minks (*Neovison vison*) were willing to exert a great amount of effort to access a swimming pool, and when deprived of pool access for 24 h, the minks' cortisol levels were roughly equal to times when they were not fed for 24 h (Mason et al., 2001). Cows (*Bos taurus*) also exerted similar amounts of effort to access a pasture as they exerted to access to fresh feed, which demonstrates their desire to engage in grazing behavior outdoors (von Keyserlingk et al., 2017). The latter two studies indicate that animals value performing certain natural behaviors (e.g., swimming, grazing) as much as consuming food itself, suggesting the inability to perform these behaviors would have a negative impact on welfare.

Naked mole rats (*Heterocephalus glaber*) are a common species in zoos; at the time of writing the zoo-based population is over 3500 globally (Species360 Zoological Information Management System, 2023). Naked mole rats are well adapted for digging, evidenced by their large incisors for chiseling out dirt and whiskers between their toes for sweeping dirt away, and this behavior is key to their survival in the wild. Naked mole rats are native to East African desert environments (Djibouti, Ethiopia, Kenya, and Somalia) and are completely fossorial. Following rains, wild naked mole rats rapidly expand their tunnel system to search for food, mainly roots and tubers, that will have to last the colony until the next rain makes it possible to expand again (Jarvis et al., 1994). Naked mole rat colonies build underground chambers for specific uses, such as food storage, young rearing/nursing, denning, and waste storage, and tunnels are built not just to connect these chambers, but also to search for new food sources and expand for a growing colony population (Sherman et al., 1991). A typical, wild naked mole rat colony consists of 70–80 individuals, and it is estimated that a single colony can dig 400–500 mole hills per year, displacing an equivalent of 3.6–4.5 tons of soil per year (Brett, 1986). A complete system of tunnels and chambers can be over 3 km in length (Brett, 1986).

Research Highlights

When zoo-housed naked mole rats were provided a moveable substrate for digging, exploration increased, and barrier-directed behavior decreased. These changes likely indicate that fulfilling the natural motivation to excavate improved welfare.

Naked mole rats are eusocial, defined by the occurrence of overlapping adult generations with divisions in labor and a singular dominant breeding individual, typically a female, often referred to as the "queen" (Burda et al., 2000; Buffenstein et al., 2012). Most individuals are workers, either gathering food, building the living structure, or rearing young, while the queen reproduces with one to three males. In naked mole rats, roles are strictly and aggressively reinforced, especially by the queen (Clarke & Faulkes, 2001) However, workers also reaffirm their roles behaviorally by performing their designated tasks, which is primarily tunnel and chamber construction (Clarke & Faulkes, 2001). Despite this strict hierarchy, the naked mole rats themselves do not show elevated stress hormones with this structure, and in fact, individuals that have been removed from the colony show elevated stress hormones (Edwards et al., 2020). The expression of this social structure, and the roles within it, enables naked mole rats to survive in the harsh environments in which they evolved. Therefore, tunnel design and construction are the foundation for the social structure and survival of a colony, and digging behavior is very likely a highly motivated behavior that, when expressed, can support positive welfare.

Traditional zoo housing practices for naked mole rats do not provide opportunities for tunnel construction, although some colonies are offered various bedding materials, such as paper strips, corn husks, wood shavings, or vermiculite (Buffenstein et al., 2012). Throughout zoos, naked mole rats are typically housed in a system of gunite-lined acrylic chambers connected with acrylic tubes. Visually, these artificial habitats resemble the chamber and tunnel systems naked mole rats create in their natural environments, but they do not allow for naked mole rats to dig to excavate or connect these tunnels and chambers. This may also mean that there is little need for the division of labor that underlies this species' social structure.

With our study, we aim to evaluate the changes in zoo-housed naked mole rat behavior when granted the opportunity to dig and engage in natural tunnel construction, and the potential impacts this could have on animal welfare. We consider exploratory behavior, digging behavior, and affiliative behaviors to be positive welfare indicators, and barrier-directed behavior and aggressive behavior to be negative welfare indicators. Exploratory behaviors were of interest as they are natural behaviors that are presumably associated with a high degree of motivation given their role in tunnel construction, and therefore, an increase in these behaviors could also indicate an improvement in welfare. Exploration can also benefit cognitive stimulation and indicate a level of comfort and safety in the

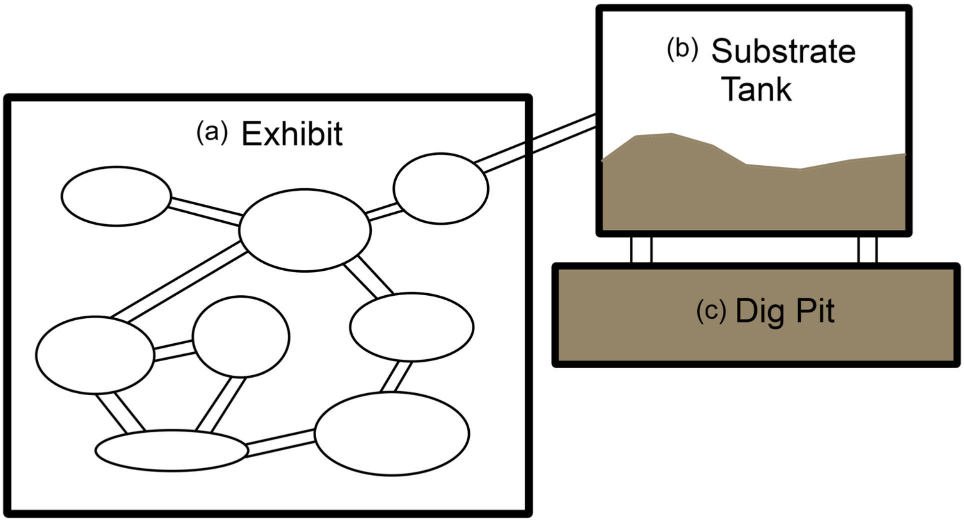

FIGURE 1 Diagram of treatment housing features. During the control condition, the naked mole rat colony had access only to the exhibit (a). During the loose substrate tank condition, the colony had access to the exhibit and the substrate tank (a + b), and during the dig pit condition, they had access to the exhibit, substrate tank, and dig pit (a + b + c). [Color figure can be viewed at wileyonlinelibrary.com]

environment (Keeling, 2018)—other signs that exploratory behaviors are linked to positive welfare. To further evaluate the potential impact on welfare, we also considered changes in barrier-directed behavior, such as unproductive digging and chewing on walls, across treatments, as this behavior has been speculated to be indicative of frustration in other species (Bashaw et al., 2007; Mason & Burn, 2018) and a decrease in these behaviors could be indicative of an improvement in welfare. Social behaviors were of interest both to understand behavioral changes associated with the opportunity to perform roles in this eusocial structure and because of their relationship to welfare; an increase in aggression could be associated with welfare compromise whereas an increase in affiliation could be associated with improved welfare (Keeling, 2018). We hypothesize that providing a space and substrate for the naked mole rats to dig would be associated with increases in digging and exploration and decreases in barrier-directed behaviors. We also consider how observed behavioral changes persist over days given that the opportunities provided by the substrates change as the substrate is utilized.

2 | METHODS

2.1 | Subjects

This study focused on one naked mole rat colony visible to the public at Lincoln Park Zoo (Chicago, IL, USA). The group size ranged from 24 to 26 individuals due to two deaths that occurred during the course of the study. All individuals were born in captivity and were not individually identifiable As such, specific ages are not known, but the colony arrived at Lincoln Park Zoo in 1996 from another zoo accredited by the Association of Zoos and Aquariums, and there were six individuals born in December 2020. Animal care staff service the exhibit daily to offer fresh food, and the frequency of cleaning depends on need, with the most used chambers cleaned three times per week. The colony receives a diet of rodent pellets, sweet potatoes, lettuce, carrots, parsnips, and turnips. Enrichment is offered daily and includes a variety of objects and substrates to stimulate exploration and surface-level digging, such as dry, loose sand. The care protocol for the naked mole rat colony did not change during the study.

2.2 | Treatments

For the purpose of this study, we focus on three treatments: traditional housing ("Control"), traditional housing with access only to the loose substrate tank ("Substrate Tank"), and traditional housing with access to the dig pit and associated loose substrate tank ("Dig Pit"). Before the start of the study, to identify a dig pit model that was safe and feasible for animal care, the naked mole rats were exposed to multiple iterations of a dig pit. The main safety concern was due to the weight of the digging substrate—when hydrated, the substrate in the dig pit weighed about 55lbs. While a densely packed substrate is needed in order for the naked mole rats to create tunnels, this also creates a great risk in the case of tunnel collapses. To minimize this risk, we opted for a dig pit model that was wide and shallow. Although this limited the mole rats to digging in a shallow depth, there was no possibility of a tunnel collapse that would be too heavy for the mole rats to dig themselves out of. Adding the substrate and dig pit to the exhibit sequentially also gave the mole rats time to learn there was a new area to which they had access.

In the Control, the naked mole rats were housed in the unmodified exhibit that consists of 12 acrylic chambers (ranging from 14″ × 10″ × 14″ to 14″ × 10″ × 10″) lined with gunite and connected by acrylic tubes (2-inch diameter) (Figure 1). During Substrate Tank Treatment, the naked mole rats had access to their regular exhibit space and, via additional acrylic tubes, to a 24″ × 13″ × 16″ acrylic tank filled with approximately 2 inches of dehydrated ZooMed Excavator Clay Substrate. This amount allowed the naked mole rats the opportunity to move the substrate around, but the substrate was too shallow and loose for actual tunnel construction and cooperative excavation. During the Dig Pit Treatment, acrylic tube connections were added to the exhibit to provide naked mole rat access to a "dig pit" acrylic box (30″ × 20″ × 2″) with two circular openings in the top for the naked mole rats to enter and exit (Figure 1). Access to the dig pit was only possible through the portals in the bottom of the substrate tank (Figure 1). During the control, all of the naked mole rats were frequently seen sleeping in the nesting chamber together which is smaller than both the loose substrate tank and dig pit, so we have confidence the entire colony could occupy the substrate tank and dig pit simultaneously. The top of the acrylic box that housed the dig pit was fitted with hinges to allow care staff to open the box and access the inside to clean and repack the substrate. This hinged top also served as an important safety feature allowing keepers to access animals inside the box. Densely packed, hydrated ZooMed Excavator Clay Substrate filled the acrylic box to provide the naked mole rats a digging substrate that allowed for tunnel construction. Above the dig pit we placed the loose substrate tank aligned with the circular openings to the dig pit. This substrate tank served as a necessary reservoir for the excavated substrate as well as a connection to the exhibit (Figure 1). Both the dig pit and substrate tank were visible from the public viewing area. For all treatments, the ambient environment was kept consistent at 80–82°F and 45%–60% relative humidity as per usual husbandry.

2.3 | Data collection

We collected data for 10 days in each of the three treatments sequentially (Table 1). Observations were conducted between 9AM and 5PM while the building was open to visitors, and observation times were balanced across all hours for each treatment period. On each observation day, we conducted 10 consecutive 5-min focal observations on randomly selected individuals with 30-s intervals between point samples, using a comprehensive ethogram (Table 2). The ethogram was designed based on published ethogram specific to naked mole rats (Lacey et al., 1991) and the primary ethogram used at Lincoln Park Zoo. The mole rats are not individually identifiable, and therefore, it was not possible to guarantee each focal was on a unique mole rat. The random selection of the focal mole rat was accomplished by counting the mole rats left to right across the habitat and selecting the individual in the position identified by a random number generator that varied between one and the total number of mole rats. In addition to the behaviors scored on 30-s intervals, social interactions were scored on an all-occurrence basis (Table 2). The all-occurrence behaviors were chosen in advance to ensure brief, yet meaningful, behaviors that would be unlikely to be captured on the 30-s point scans would be documented. Immediately after the focal observations, we completed one group observation. During the group observation, we counted the number of naked mole rats which were inactive, digging, or performing another active behavior in each chamber of the exhibit (Table 3). Focal and group observations were electronically recorded using the ZooMonitor app (Wark et al., 2019), and all observations were conducted from the public viewing area. All of the chambers, the substrate tank, and the dig pit were visible from the public viewing area; however, the tubes connecting the chambers were not visible during observations.

Data were collected by a single observer who had established interobserver reliability with a second observer by achieving 85% agreement across three consecutive observations.

TABLE 1 Treatments.

Treatment	Date range	No. of 5-min follows	No. of animals in colony
Control	October 4–15, 2021	100	26
Loose substrate tank	January 31–February 11, 2022	100	26
Dig Pit	August 10–23, 2022	99	24

2.4 | Data analysis

To evaluate the changes in naked mole rat behavior across treatments, we compared the proportion of exploratory behaviors, barrier-directed behaviors, and aggressive and affiliative social interactions across treatments. Reproductive behavior was not included as it was only observed once during the entire study. Aggressive interactions included contact and noncontact aggression. We also considered digging behavior across treatments, as well as across days post-provisioning of the substrate tank and dig pit. Analyses for digging behavior were handled differently given that digging was not feasible during the Control treatment (with the exception of 1 day of sand enrichment). Scans on which focals were not visible were excluded from the analysis (7.2% of scans). For data collected during group observations, we provide descriptive results.

Data collected during focal follows were analyzed in R (R Core Team, 2021) and we used a Bayesian framework to parameterize our models. We opted to use a Bayesian framework for three reasons. First, Bayesian models simplify accommodation of this study design because one can specify and estimate random effects within the model (Gelman et al., 2013). Second, Bayesian models are increasingly used to address questions in behavioral ecology (Gallo et al., 2022; Gerber et al., 2024; Murray et al., 2021; Rivera et al., 2022). And third, the posterior distributions of model parameters that Bayesian analysis generates are probability distributions, which makes it far simpler to interpret and quantify uncertainty

TABLE 2 Individual focal ethogram.

Category	Behavior	Definition
Other	Inactive	Animal is stationary and not engaged in an active behavior listed.
	Feeding/drinking	Animal is chewing and ingesting food items or manipulating a food item for the purpose of feeding.
	Locomotion	Animal is moving at least one body's length in non-stereotypical manner (modifiers: n/a, pass over, pass under).
	Digging[a]	Animal is using their body in repetitive manner to excavate substrate (typically forelimbs but may include hind legs or snout) (modifiers: substrate, type of digging).
	Self-maintenance	Animal is performing any comfort related behavior including self-directed behaviors, stretching, yawning, rolling, wallowing, or rubbing against objects.
	Scent-marking	Animal is intentionally marking an area using bodily fluids, including urine, feces, and glandular secretions. Includes all behaviors involved in marking, as well as secondary behaviors to spread scents (e.g., feet scraping) and visually indicate scents (e.g., clawing).
	Elimination	Excretion of body waste in a non-scent marking manner (i.e., not spraying urine or spreading feces over a specific target area).
	Affiliative[a]	Animal performs any nonsexual affiliative behavior, including grooming a social partner, playing, or social greetings.
	Contact aggression[a]	Animal physically attacks another individual, including biting, batting, or kicking.
	Noncontact aggression[a]	Animal performs noncontact aggressive behavior towards another individual, including threat displays or chasing.
	Reproductive[a]	Animal is engaged in courtship or sexual behavior with another individual [Note: please specify whether the focal animal was the initiator or recipient].
	Other	Animal is performing any behavior not listed [Note: please specify the behavior category and make a comment to describe behavior].
Barrier-directed	Barrier-directed[a]	Animal is interacting with barrier (i.e., gnawing on walls or acrylic).
Exploratory	General exploration	Animal is visually inspecting or sniffing the substrate in a non-focused manner.
	Focused Investigation	Animal is actively sniffing or pawing at a specific area within ½ body's length.
	Object manipulation	Animal is moving a non-fixed object in enclosure using mouth or paws. [Note: If object is associated with food, score as Feed/Forage/Drink. If animal plays with object, score as Solitary Play]
Not visible	Behavior obscured	The behavior of the animal cannot be determined but the location of the animal is known.
	Animal not visible	The animal is completely not visible and its location is unknown.
Nearest neighbor proximity	Contact	Animal is in physical contact with another individual.
	Proximate	Animal is within 1 body's length of another individual.
	Distant	Animal is greater than one body's length away from the nearest individual.

[a]Behavior also scored on all-occurrence basis.

(Gelman et al., 2013). As with all Bayesian analyses, we specify prior distributions for model parameters to fit them, which can be used to incorporate prior information about the range of values a specific parameter may take. As we had no prior information for this study, we used standard, or “vague” priors for all model parameters, which we detail below. The use of vague, or non-informative, priors is common as such priors have a minimum influence on the posterior, and instead allow the data to have the strongest influence on parameter estimates (Gelman et al., 2013).

TABLE 3 Group observation ethogram.

Behavior	Definition
Digging	Animal is using their body in repetitive manner to excavate substrate (typically forelimbs but may include hind legs or snout).
Inactive	Animal is stationary and not engaged in an active behavior listed.
Other active	Animal is performing any behavior not listed.

For behaviors recorded on the interval, we fitted multinomial models, treating 'other' behaviors as the baseline category that barrier-directed and exploratory behavior were compared against. Multinomial models are a generalization of binomial models (e.g., logistic regression) when the number of categories is greater than two. As we had three behavioral categories (i.e., other, barrier-directed, and exploratory), multinomial models represented a natural choice to address our hypotheses because they can incorporate both continuous and categorical covariates as independent variables. This meant that this model could be used to evaluate changes in barrier-directed and exploratory behavior relative to "other" behaviors about which we did not have predictions under different treatments, which was an objective in our study.

The response variable for this analysis was a vector of counts for each behavior, and each observation had its own vector of counts. We fitted three models to these data. The first model included treatment as an independent variable (i.e., control, dig pit, or substrate), which allowed us to estimate how the different treatments were associated to increases or decreases in barrier-directed and exploratory behavior relative to the "other" behavior category we used as a baseline because they were not of a priori interest in this study. The second model included treatment and trial day as independent variables. This second covariate was included to determine if there were diminishing returns for a given treatment over time (e.g., if the dig pit is fully excavated at some point over the 10 trial days). The third model was the null model, which assumed all behaviors did not vary due to treatment. All parameters were given vague Logistic (0,1) priors.

To quantify whether our treatments were related to an increase or decrease in affiliative or aggressive behaviors (Table 4) we used Poisson generalized mixed models. We used this modeling framework as our occurrence behavior data were count data (i.e., the number of times a given behavior was observed in the focal mole rat over a 5-min period). We fitted three models to each behavior, all of which included an observation ID as a random effect. The first model included treatment as an independent variable while the second model was a null model. All parameters were given vague Normal (0, 2) priors, while for the j in $1, \dots, J$ observations the random effect was Normal(0, σ) where $\sigma \sim \text{Gamma}(1, 1)$. All models were fitted in nimble v 0.12.2 (de Valpine et al., 2017) in R v 4.2.0 (R Core Team, 2021). Following a 10,000 step burn-in, posteriors were sampled for a total of 190,000 times across 2 chains. We ensured the posteriors converged for each parameter by visually inspecting traceplots and ensuring Gelman-Rubin diagnostics were < 1.1 (Gelman et al., 2014). For each model set, we compared the relative fit of each model using WAIC, a Bayesian formulation of AIC, and considered any model within 2 ΔWAIC of the best-fit model competitive (Gelman et al., 2014). Following this, we determined if 95% credible intervals bounded zero to evaluate evidence of an effect for our model parameters.

TABLE 4 Model selection results for behavior analysis. Models were compared using WAIC, and the ΔWAIC column shows the difference in WAIC values relative to the model with the lowest WAIC.

Analysis	Model	ΔWAIC
Interval behaviors	Treatment + Day	0
	Treatment	36.38
	Null	44.28
Affiliative behaviors	Treatment	0
	Null	1.34
Aggressive behaviors	Treatment	0
	Null	2.59

To characterize changes in digging behavior across treatments, we only considered the Substrate Tank and Dig Pit treatments given that opportunities for digging were virtually absent in the control treatment. We fitted a Bayesian logistic regression mixed effects model to these data. Our binary response variable was whether or not naked mole rats were observed digging during a scan. For fixed effects, we included a binary dummy variable that equaled 1 if a data point was associated with the Dig pit treatment and was otherwise zero as well as the day number of an observation. We also included observation as a random intercept in our model. This model was compared against a null model that excluded our two fixed effects via ΔWAIC.

This study was approved by the Lincoln Park Zoo Research Committee (Project # 2021-012).

3 | RESULTS

The results of the group scans revealed that the average percent of the colony (refer to Table 1 for total colony population for each condition) digging, inactive and engaged in other behavior across treatments was: Control: 0.13 ± 0.13% digging; 36.4 ± 7.33% inactive, 7.66 ± 0.84% other behavior; Substrate Tank 1.44 ± 0.69% digging; 19.5 ± 2.94% inactive, 7.08 ± 2.00% other behavior; Dig Pit: 1.55 ± 0.51% digging, 19.1 ± 3.11% inactive, 7.16 ± 1.11% other behavior. The digging observed in the Control was a result of the provisioning of sand enrichment in one chamber on one observation day. Further comparisons of digging between the Substrate Tank and Dig Pit are provided below. Note that the low proportion of individuals digging is also influenced by decrease in digging over treatment days, as detailed below.

During focal follows, we observed 102 barrier-directed, 211 exploratory, and 2285 other behavioral events across all treatments. We found that the best-fit model included treatment and trial day (Table 4). Exploratory behavior increased when naked mole rats had access to the dig pit ($\beta_{\text{exploratory, dig pit}} = 0.99$, 95% CI = 0.65, 1.34) but did decrease over trial days ($\beta_{\text{exploratory, trial day}} = -0.19$, 95% CI = −0.24, −0.13). At the start of the study—when naked mole rats were given access to the dig pit—the probability they showed exploratory behavior was 0.26 (95% CI = 0.20, 0.33; Figure 2). At the end of the study, this probability decreased to 0.06 (95% CI = 0.05, 0.09). We failed to find an effect of loose substrate on naked mole rat exploratory behavior ($\beta_{\text{exploratory, substrate}} = 0.05$, 95% CI = −0.33, 0.43). Overall, exploratory behavior occurred most when naked mole rats were given access to the dig pit, though the rate at which

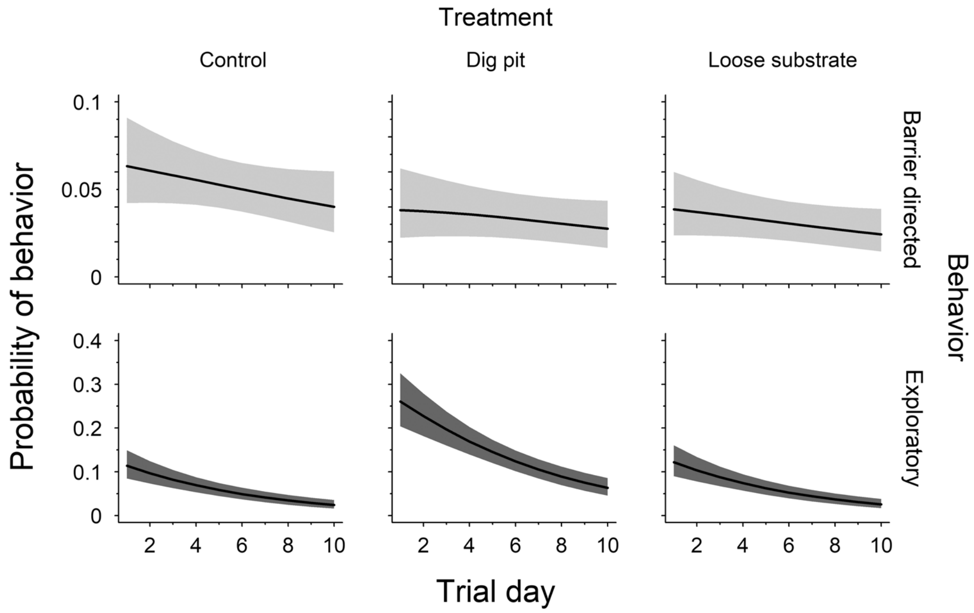

FIGURE 2 Probability of behavior by treatment across trial day. The solid line represents the probability of the behavior across the 10 trial days, and the shaded gray areas represent the 95% credible intervals.

exploratory behavior decreased over time was also the greatest under the dig pit treatment (Figure 2).

Barrier-directed behavior was negatively associated with having access to loose substrate ($\beta_{\text{barrier directed, substrate}} = -0.51$, 95% CI = −0.99, −0.05), that is, the presence of loose substrate was associated with less barrier-directed behavior. There was some evidence that barrier-directed behavior also decreased over time ($\beta_{\text{barrier directed, trial day}} = -0.07$, 95% CI = −0.14, 0.01). As the relationship between trial day and barrier-directed behavior was weaker than trial day and exploratory behavior, the rate at which barrier-directed behavior declined over the study was also smaller. At the start of the study—when naked mole rats were given access to the loose substrate—the probability they showed barrier-directed behavior was 0.04 (95% CI = 0.02, 0.06; Figure 2). At the end of the study, this probability decreased to 0.02 (95% CI = 0.01, 0.04). We failed to find an association between barrier-directed behavior and naked mole rat access to the dig pit ($\beta_{\text{barrier directed, dig pit}} = -0.34$, 95% CI = −0.85, 0.14). Overall, while barrier-directed behavior was rare, it was most common when naked mole rats did not have access to either the dig pit or loose substrate (Figure 2).

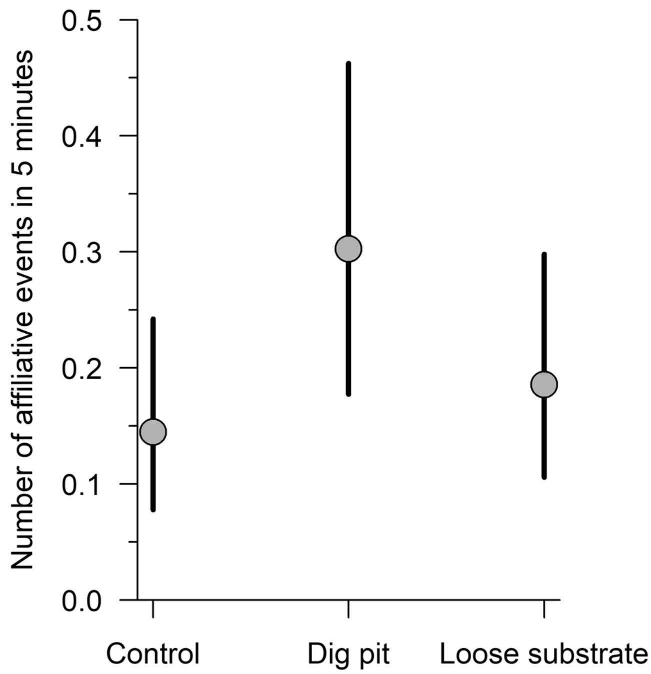

FIGURE 3 The estimated rate of affiliative interactions per 5 min by treatment. Gray dots represent the median estimates while the vertical lines are 95% credible intervals.

3.1 | Social behavior analysis

3.1.1 | Analysis of affiliative interactions

For the affiliative analysis, the null model was within 2 ΔWAIC of the treatment model, which was largely driven by the minimal effect that loose substrate had on affiliative behavior ($\beta_{\text{substrate}} = 0.25$, 95% CI = −0.38, 0.90). However, affiliative behavior increased when naked mole rats were provided access to the dig pit ($\beta_{\text{dig pit}} = 0.73$, 95% CI = 0.15, 1.34). As such, we made inference with the top model, as only one parameter in our treatment was uninformative. When provided access to a dig pit, affiliative behavior increased 2.08 times (95% CI = 1.17, 3.81) relative to the control (Figure 3).

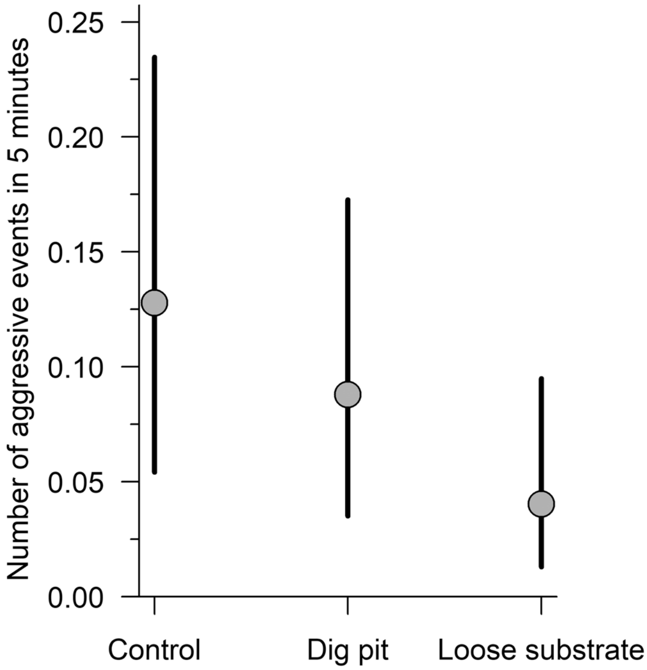

FIGURE 4 The estimated rate of aggressive interactions per 5 min by treatment. The gray dots represent the median estimated values, and the lines represent the 95% credible intervals.

3.1.2 | Analysis of aggressive interactions

For the aggressive behavior analysis, the model that included treatment was the only competitive model (Table 4). As with the affiliative analysis, aggressive behaviors were rare, but we did detect a decrease in aggressive behaviors when mole rats were provided loose substrate ($\beta_{substrate} = -1.14$, 95% CI = −2.16, −0.24). We failed to detect a difference in aggressive behavior when mole rats had access to a dig pit ($\beta_{dig\ pit} = -0.37$, 95% CI = −1.15, 0.39). Again, aggressive social behaviors were still observed less than once per 5-min trial; however, they were least common when the naked mole rats had access to the tank of loose substrate. For example, providing access to loose substrate decreased aggressive behaviors by a factor of 3.13 (95% CI = 1.27, 8.63) relative to the control. Providing access to either a dig pit or loose substrate, on average, reduced aggressive behaviors about 1.94 times (95% CI = 0.98, 3.82) relative to the control, standard housing (Figure 4).

3.1.3 | Digging analysis

With regard to digging behavior, the model including condition outperformed the null model (posterior estimates included in Table 5). We failed to detect a difference between the Substrate Tank and Dig Pit Conditions, and the probability of detecting digging on any scan was 0.04 (95% CI = 0.01, 0.13) (Table 5). This low probability is related to the duration of the treatments, as we found an association between digging and treatment day indicating that naked mole rats were more likely to dig early in treatments soon after the dig pit and substrate tanks were made available, and digging decreased over time (Table 5).

TABLE 5 Results of analysis comparing digging in substrate tank and dig pit conditions.

Parameter	Estimate	Credible interval 2.5%	Credible interval 97.5%
Intercept	−3.22	−4.81	−1.86
Dig Pit	0.16	−1.36	1.65
Day Number	−0.76	−1.17	−0.46

4 | DISCUSSION

The opportunity to fulfill motivations for certain natural behaviors is key to promoting great welfare for animals living in captivity (Veasy 1996; Bracke & Hopster, 2006; Fraser, 2008; Mason & Burn, 2018). Therefore, the exhibits or spaces these animals live in must be designed in a way that provides these opportunities. Given this link, we set out to determine whether providing movable substrates in different manners—and therefore, the opportunity to fulfill a natural motivation to dig—would influence the behavior and welfare of a zoo-housed naked mole rat colony. First and foremost, digging behavior that was virtually absent in the historical, standard housing was expressed once movable substrates were offered, demonstrating that the naked mole rats were motivated to express this behavior and chose to do so when the opportunity was provided by more natural housing treatments.

We took a close look at exploratory and barrier-directed behavioral changes across different housing conditions. During the treatments that presented naked mole rats with access to movable substrate, exploratory behavior increased, demonstrating that the naked mole rats did indeed explore the new spaces with both olfactory behaviors (sniffing) and tactile exploration (pawing, touching with whiskers). Interestingly, although exploratory behaviors were most often expressed within the additional dig pit and loose substrate tanks, we noticed that naked mole rats' exploratory behavior in the standard housing chambers increased during the two treatments that allowed access to movable substrates. It appeared that access to the dig pit or loose substrate tank may have introduced new scents into the exhibit which led to an increase in exploratory behavior, or potentially that the discovery of a new addition on to the exhibit sparked further exploration for new spaces.

Barrier-directed behaviors, mainly unproductive digging, are likely a potential sign of frustration (Mason & Burn, 2018) and were less common during treatments that allowed the naked mole rats access to the movable substrate. This impact was present with both the loose substrate and the dig pit but was most pronounced with dig pit access. It appeared that when given opportunities to perform functional digging behavior to relocate substrate and excavate tunnels, the naked mole rats opted for functional digging and excavation, reducing the expression of a similar, unproductive motor pattern that had taken the form of chewing and pawing at exhibit walls.

Access to movable substrate, either in the loose substrate tank or the dig pit, was also correlated with increased affiliation and decreased aggression. Most of the affiliative behaviors observed were social greetings (such as nose pressing, nuzzling, and ano-genital sniffing). Naked mole rats identify other members of the colony by all having a shared, colony scent, and while this is typically achieved by all members rolling in the same toilet chamber (Buffenstein et al., 2012), they may have used the substrate as a new scent by which to identify themselves. The affiliation may have also resulted from increased communication underlying the cooperative excavation activities. We can only speculate about why aggression decreased with access to the movable substrate, however, it may be that the naked mole rats were redirecting or reallocating energy that would have been spent on conflict to the productive activity of digging, or that the added space of the substrate tank and dig pit allowed for more conflict avoidance. Overall, the number of aggressive interactions was higher than affiliative interactions, but given the strict, hierarchical social dynamics within this eusocial species, the higher rate of aggression is not unexpected or abnormal (Buffenstein et al., 2012; Clarke & Faulkes, 2001).

Aggression was lowest with access to the loose substrate tank (without the dig pit). Though the dig pit gave the naked mole rats another task to perform, naked mole rats were often in close proximity to each other and working together to excavate tunnels, whereas the loose substrate tank was more open and allowed more individualized work. Although aggression was not reduced in the dig pit treatment compared to the control, the ability for the mole rats to more closely replicate the natural behaviors of cooperative, assembly-line-style digging to build tunnels, along with increased exploratory behavior and decreased barrier-directed behavior, indicates that the welfare benefit of the dig pit is probably greater than just a loose substrate tank alone. Frequency of aggression was also still lower with access to the dig pit than traditional exhibit housing. Overall, increased socialization for such a highly social and cooperative species likely indicates positive welfare, demonstrating that access to movable substrate, specifically in a set-up where it is a challenge to excavate and requires "teamwork," likely improves the welfare of naked mole rats.

During the study, it quickly became apparent that the speed at which the naked mole rat colony could empty the dig pit had been underestimated—in general the dig pit was excavated fully in the first day. After emptying the dig pit, behavioral patterns for both exploratory behaviors and barrier-directed behaviors drifted back towards those observed during traditional housing with no access to movable substrate, leading to a decrease in exploratory behavior and increase in barrier-directed behavior. While the fluctuation between periods of high activity expanding the tunnel system and low activity resting is akin to what is seen in wild populations between wet and dry seasons (Jarvis et al., 1994), zoo-housed populations would likely benefit most from a shorter period between refilling the dig pit. Mixing, refilling, and packing the substrate in the dig pit was time intensive and required heavy lifting by the animal care staff. For a moveable substrate dig pit to be a regular, sustainable addition in a naked mole rat exhibit, the time and effort required by animal care staff to reset the dig pit would need to be balanced with how quickly the mole rats are able to empty the dig pit.

There are a few ways a similar study could be improved in the future. First, some visibility was limited by observations being conducted from the public viewing area as there were times when the focal mole rat was not visible due to either going in the tunnels out of view or being obscured by other mole rats. Future studies could benefit by using sensors or cameras to track animals entering or exiting the dig pit. We also heard more vocalizations from the colony during dig pit access, so tracking and analyzing the different vocalizations could potentially also be useful for measuring the colony's reaction to the dig pit. Additionally, it would be good to understand the effects of visitors on the naked mole rat behavior and to understand the value of the additional space provided in the Substrate Tank and Dig Pit conditions.

Because we were unable to individually identify the naked mole rats, our behavioral analysis is limited to the colony level; however, previous research has found that the larger mole rats, especially the breeding female and males, do less digging and tunnel construction than the smaller "worker" mole rats (Clarke & Faulkes, 2001). While we noted that there tended to be a size difference in the smaller mole rats using the dig pit most often and the larger mole rats staying in the nesting chamber, we were not able to confirm specific individuals or individualized characteristics (i.e. age, sex). Behaviors analyzed at the colony level indicate that the dig pit improved welfare for the colony, but an individualized analysis of dig pit use could offer additional insight into colony social dynamics and potentially determine which roles in the colony benefit the most from dig pit access.

There is a strong link between the ability to perform natural behaviors and good welfare (Veasy, 1996, 2017; Fraser, 2008), and there is evidence in multiple species that shows improved welfare when given access to spaces that provide opportunities to perform these natural behaviors (Bryan et al., 2017; Smith et al., 2023). Naked mole rats evolved adaptations for digging and unique eusociality to survive in harsh environments (Jarvis et al., 1994; Brett, 1986), indicating a strong natural motivation to perform these behaviors. Results of this study indicate that the colony's welfare benefited from access to movable substrate which provided the opportunity to perform natural behaviors, like tunnel construction and excavation. Social interaction in the colony also increased during access to movable substrate, which may indicate a cascading impact on welfare when captive housing conditions better resemble natural environments and better offer opportunities for a species' natural behavioral repertoire.

We hope that this design can be a guide for other institutions to provide their naked mole rats a safe and sustainable opportunity to perform natural behaviors. Future research into this topic may contribute not only to a better understanding of the behavior and welfare of a unique and understudied species, but also the role natural behaviors play in improving welfare.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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