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Characterization of a Jumping Stereotypy in Gerbils (*Meriones unguiculatus*) and Assessment of Opaque Tubing Enrichment on Stereotypies and Breeding

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Mongolian gerbils can develop stereotypic behaviors, including corner digging. At our institution, gerbils also engage in repetitive corner jumping, which we sought to characterize as a potentially novel stereotypy in gerbils. We then attempted to mitigate this behavior by mimicking the natural habitat by adding intracage environmental complexity. Seventeen gerbil breeding pairs were video recorded in their home cages during the light cycle. Repetitive corner jumping and digging were compared between different times of day to assess when the behaviors occurred and whether they were temporally associated. To determine whether we could reduce the incidence of stereotypic behaviors, we tested a straight tube or 1 of 3 angled opaque tubes in different orientations, which were fitted to the gerbils' preexisting opaque nesting box. Behavior was assessed at baseline and at 1, 4, 8, and 12 wk to evaluate opaque tube placement as an intervention. In addition, breeding efficiency, valuated as the number of gerbil pups born and weaned per breeder pair, was compared with pre- and poststudy data. The number of corner jumps was highest at the end of the light cycle and the majority were associated with corner digging. After placement of the enrichment tubes, an initial increase in corner digging behavior was observed and persisted throughout the study period. The opaque tubes were not associated with significant changes in corner jumping. After adjusting for age, the addition of opaque tubing to gerbil breeding cages was not associated with significant changes in breeding efficiency. The addition of opaque tubing did not effectively address concerns about stereotypic behaviors and was associated with a chronic increase in stereotypic corner digging among breeding gerbil pairs.

Abbreviations: BORIS, Behavioral Observation Research Interactive Software

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Introduction

The Mongolian gerbil (*Meriones unguiculatus*) has been used as a model for over 70 y in a wide array of research including aging, auditory and visual function, epilepsy, and gastrointestinal disease.[3-5,7,12,15,16] *M. unguiculatus* is native to Mongolia and northern China, where it lives in family groups in burrows in dry soil or agricultural fields.[2] A catalogue of the captive and natural behaviors of Mongolian gerbils was compiled in 2015, detailing 116 specific behaviors.[17] Of all the behaviors described, only 2 stereotypies were identified: stereotypic digging and bar-gnawing. A stereotypy is characterized as a morphologically identical movement that is regularly repeated, and seems purposeless or aberrant.[24] Stereotypic digging was defined as digging composed of 7 or more scratches or digging lasting longer than 12 s.[17] Bar-gnawing was defined as grasping a bar from the enclosure between the gerbil's teeth and moving the mouth up and down the bar while chewing.[17]

Stereotypic digging in laboratory gerbils was first documented in the 1990s; the behavior begins to develop at 24 d of age, prior to weaning.[33,34] Stereotypic digging is not triggered by small cage size, as a 4-fold increase in cage size did not prevent the behavior.[34] The addition of an ethologically relevant digging substrate like dry sand did not significantly reduce stereotypic digging either.[34] However, providing an artificial burrow made of 2 nest chambers and several tunnels did significantly reduce stereotypic digging.[35] This latter finding suggests that the motivation to dig is driven by the goal of having a burrow-like shelter. Furthermore, if the tunnel did not lead into a sheltered nest area, gerbils still developed stereotypic digging.[35] Juvenile gerbils housed in opaque burrows develop significantly fewer stereotypies than those housed in transparent ones.[29] An artificial burrow that includes a separation wall, an angled access tube, a transparent box, and an opaque nest-box and is designed to fit inside a standard cage is reported to be efficacious in reducing stereotypies in gerbils.[29,30]

Stereotypies are commonly used as markers of welfare in research animals and are often observed when rodents are housed under barren conditions.[18] At our institution, gerbils are observed repetitively digging and vertical jumping at the cage corners. To our knowledge, stereotypic jumping in gerbils has not previously been reported in the literature. Stereotypic

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jumping behaviors have been reported in other rodents (bank voles, *Clethrionomys glareolus*) housed in barren cages and can be reduced in frequency by the addition of naturalistic cage enrichment.[25,26] Bar gnawing is not observed in our colony. The breeding gerbils at our institution are provided an opaque nest-box with a single open doorway entrance and shredded paper nesting material. We sought a practical, low-cost solution that could provide the gerbils a more burrow-like entrance. We hypothesized that a removable PVC tube segment in different shapes ('Straight', 'L', 'T', or 'XYZ') added to the gerbils' nest-box would decrease the incidence and duration of stereotypic digging and jumping (Figure 1). In addition, we assessed whether the additional enrichment affected breeding efficiency.

Materials and Methods

Animals and housing. Mongolian gerbils were initially obtained from Charles River Laboratories (Wilmington, MA) in 2010 to establish a breeding colony. Intermittently new gerbils from the same source were introduced to the colony to prevent genetic drift. For this study, 17 gerbil breeding pairs (4 to 20 mo) were housed in autoclaved individually ventilated caging (MultiSpecies model, 12″ W x 17.5″ D x 8″ H, Micro-VENT, Allentown Caging, Allentown, NJ) on aspen chip bedding (catalog number 7090A, Teklad Aspen Sani-chips, Envigo, Indianapolis, IN). Gerbils received hyperchlorinated (3 to 5 ppm), reverse osmosis auto-water (Avidity Science, Waterford, WI) and were fed a commercial rodent diet (Teklad 2920×, Envigo) ad libitum supplemented with 1 to 2 apple slices per week. All gerbils in breeding cages were provided with a noncommercial opaque nest box (Figure 1) and approximately 4 to 6 g of shredded brown paper (Enviro-dri, Shepherd Specialty Papers, Richland, MI) nesting material as standard enrichment. Nest boxes are made of high-density polyethylene (Sanalite). During the study, each cage was also provided with a PVC enrichment tube in one of 4 shapes (S, L, T, or XYZ, described below under Stereotypy Intervention Study and shown in Figure 1). Cage changes were performed every 4 wk with transference of the nest box to the clean cage unless it was damaged or visibly soiled.[19] The macroenvironment was maintained at 22.2 ± 1 °C (72 °F) and 30% to 50% humidity with 10 to 15 air changes per hour and a controlled 1410 h light:dark cycle (lights on at 0600, off at 2000). Soiled-bedding sentinels derived from the gerbil colony were monitored quarterly for internal and external parasites, using alternating survival and nonsurvival sampling techniques (fecal floatation, perianal tape tests, fur plucks, and direct intestinal examination). Each sentinel monitors up to 36 gerbil cages for excluded parasites, including *Aspiculuris tetraptera, Syphacia* spp., *Rodentolepis nana, Hymenolepis diminuta,* and *Dentosomella translucida*. Routine monitoring for bacterial or viral infections was not performed. All gerbils were on an IACUC-approved protocol and housed at an institution whose animal care and use program is accredited by AAALAC in accordance with the *Guide for the Care and Use of Laboratory Animals*[8] and all federal regulations.

Video recording. To record gerbil behavior in their home cages, 2 low profile cameras (SQ11, China) were positioned opposite the Micro-VENT and captured a 3 × 3 grid (one half of the rack) of gerbil breeding cages in the field of view. The use of a device that records locally using a microSDHC card helped ensure security of the video data. Although the cameras were capable of infrared nighttime recording, the infrared viewing distance did not provide an adequate view of the gerbils in their cages, so we only assessed behaviors during the light cycle.

Initial stereotype assessment. To assess baseline behavior, approximately 30 min of video were collected at approximately the same circadian times each day on 5 consecutive days, with an additional evening of data collection. Breeding pairs and offspring were monitored for digging and jumping behavior at or near the front of the cage. Behavior was assessed during 3 time periods each day: 'AM' shortly after the lights turned on in the housing room (0600 local time); 'Noon,' and 'PM' at the end of the light cycle (starting at 1930 before the lights turned off at 2000).

Evaluation of the baseline data indicated that the PM period was the most active time, during which the most stereotypy

Tube shape	Pros and Cons	# of cages
Straight Tube	simplest for husbandry checks, provides sheltered entrance	n=4
L Tube	simple angeled entrance, limited visibility for health checks	n=4
T Tube	more visibility for health checks, still provides angeled entrance	n=4
XYZ Tube	more complex angled entrance, may simulate going down into burrow	n=5

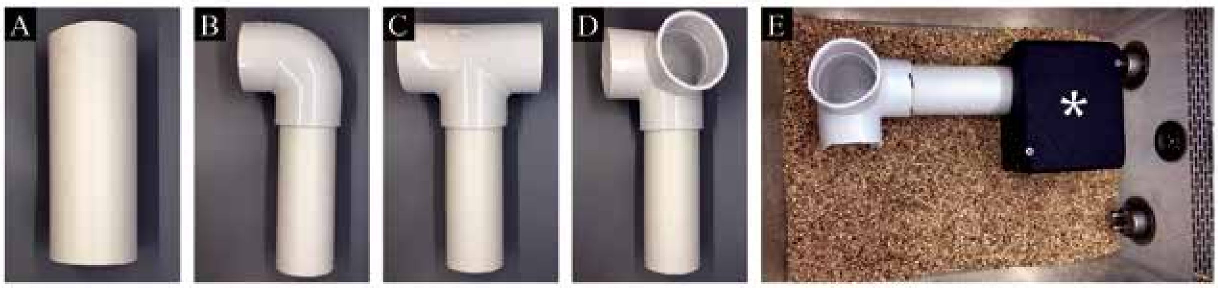

Figure 1. Enrichment tube types added to assess impacts on stereotypic behaviors in gerbil breeding cages. Description of enrichment tube shapes and number of cages with each tube shape during the study. Examples of (A) Straight tube, (B) L tube, (C) T tube, (D) XYZ tube, and (E) XYZ tube in a clean gerbil cage bottom, positioned as entrance to a gerbil nest box (asterisk).

Table 1. Stereotypic behaviors at different times of day during the baseline period.

Day	Dig Duration (s)			Number of Digs			Number of Jumps		
	AM	Noon	PM	AM	Noon	PM	AM	Noon	PM
1	14.40	—	11.50	8	0	22	44	0	69
2	—	8.95	9.68	0	1	18	0	9	48
3	10.72	7.82	13.00	7	29	103	102	167	704
4	10.65	20.62	18.75	1	7	91	5	35	604
5	8.06	12.60	10.67	10	7	38	99	29	179
Total	11.56	8.82	14.05	26	44	272	250	240	1604

Summary statistics of stereotypies during 30-min daily observation periods (AM, Noon, PM) recorded during 5 d of the baseline period. The Days column presents the number of days since starting the study. Dig Duration is the median dig duration per bout in seconds, Number of Digs is the total number of digging bouts across all gerbil pairs and the Number of Jumps is the total number of jumps across all gerbil pairs by day and time of day. Total presents the median dig duration and total number of digs and jumps by time period across the 5 d of observation.

behaviors were recorded. Thus, 6 d of the 30-min PM recordings were used to establish the baseline of stereotypic behaviors across all 17 breeding cages. This baseline was compared with the PM period of the intervention phase over 12 wk (Table 1).

During the 12 wk of intermittent experimental behavioral observation, some breeding pairs had litters at varying times. Juvenile gerbils were kept with their parents in the home cage until 28 to 30 d of age, at which time they were weaned into separate cages and were not observed during the study. The experimental unit was each breeding cage (n = 17), as adult gerbils were not always individually identifiable on the behavioral recordings.

Stereotypy intervention study. After the baseline week, all breeding cages in the study received both the opaque nest box and 1 of 4 configurations of opaque tubing made of 2-in. internal diameter PVC (schedule 40, type 1, white) piping and connectors. Gerbil breeding pairs were assigned to 1 tube type each without regard for baseline stereotypy data and with an approximately even distribution from top to bottom and left to right to control for potential differences in stereotypic behavior due to cage position on the rack. The 4 tube types, designated S, L, T, XYZ, are shown in Figure 1. The straight PVC piping segments (S), were cut inhouse to 6-in. lengths and sanded to smooth rough edges. L tubes consisted of an S segment plus an L-shaped elbow PVC connector on one end. T tubes consisted of an S segment plus a T-shaped PVC connector on one end. XYZ tubes consisted of an S segment plus a 3-way elbow connector on one end. All tube shapes were sanitized in a rack washer with a final rinse temperature of at least 180 °F.

The added enrichment tubing was not permanently affixed to the gerbils' nesting boxes. Either the box or the tubing was replaced if found visibly soiled or damaged during daily health checks. Behavioral recordings continued throughout the first week of providing the enrichment tubes and for weeklong periods (7 d) during the 4th, 8th, and 12th week of placement. (Figure 2). Both the baseline and intervention data were manually coded for the incidence and duration of stereotypic digging and productive digging, as well as the incidence of corner jumping during the last 30 min before lights out (PM period).

Behavior video coding. An open-source program, Behavioral Observation Research Interactive Software (BORIS, www.Boris.unito.it, Torino, Italy), was used to manually score recorded behaviors into quantitative data sets for 3 observed behaviors: stereotypic digging, productive digging, and corner jumping.[11] Stereotypic digging was defined based on published studies of gerbil behavior.[17,23,34,36] Specifically, digging was considered stereotypic when it lasted longer than 12 s or included at least 7 repeated forelimb movements directed at the cage wall, corner, or floor of the cage. Productive digging was defined as

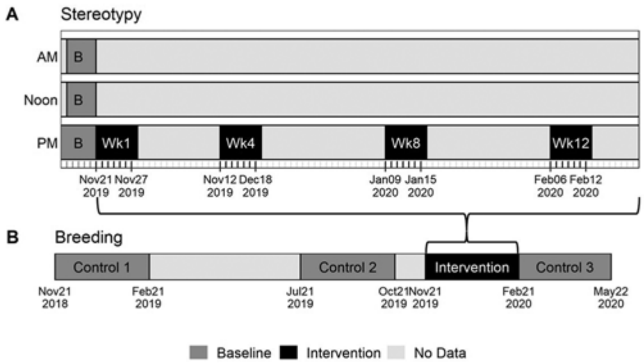

Figure 2. Schematic diagram of the study design. (A) Data collection for baseline assessment began on November 15, 2019. The date is presented on the x-axis and the 30-min daily observation period (AM, Noon, PM) is presented on the y-axis. (B) Data on the number of pups born and weaned were collected for 4 3-mo periods. Of the 17 gerbil pairs in the intervention, 9 were paired during the first control period, 14 were paired during the second control period, and 16 remained paired during the third control period. All intervention observations were recorded during the PM observation period and compared with baseline PM data only. Intervention data were collected for 7 d directly after the baseline period (Week 1) and for the 7-d intervals of 4 wk (week 4), 8 wk (week 8), and 12 wk (week 12) after the start of the study.

coordinated digging motions by the fore and hind limbs that moved bedding or nesting materials from below the gerbil to behind the gerbil.[17,23] Corner jumping events were defined as the gerbil standing on its rear limbs with forelimbs against or near the side of the cage and kicking the hind limbs to propel the gerbil vertically toward the cage lid. Using the 3 × 3 cage field of view in the recorded videos, the behaviors of up to 9 breeding gerbil pairs and their offspring could be scored simultaneously, using pause and playback features to assure scoring precision. Behaviors were scored by a single observer (LMH); this individual was not blind to the experimental treatment because the tubes were visible in the video recordings.

Statistics and data analysis. For the intervention study, the dependent variables of corner digging incidence, corner digging duration, and corner jumping incidence for each 30-min PM observation period were measured during baseline and at weeks 1, 4, 8, and 12 of the study. To assess fecundity, the number of pups born and weaned per breeding pair was compared between historical data and the 12-wk intervention period. Breeding data from these gerbil pairs over 2 separate time periods were used to establish a baseline for gerbil fecundity; Control period 1 ran from November 21, 2018 to February 21, 2019 (1 y prior to the intervention study), and control period 2 from July 21, 2019 to October 21, 2019 (3 mo prior to the intervention study). Of the 17 gerbil pairs in the behavior intervention study, 9 were paired during the first control period and 14 during the second control period. A third control period from February 22, 2020 to May 22, 2020 (after the intervention) was included to determine if age may be the primary driver of observed changes in fecundity. Three-mo breeding data collection periods were selected to include at least 2 full breeding/gestation/lactation cycles in our continuously bred gerbil colony. Breeding data are presented as pups born or weaned per 30 d to account for differences in the duration of the breeding observation periods.

Data cleaning. Because the study focused on adult gerbils, stereotypic jumping events and stereotypic digging bouts from pups were eliminated from the analysis. Thus, the primary analysis was performed on 9,118 stereotypic jumping events and 2,238 stereotypic digging bouts from 17 breeding pairs. On January 3, 2020, between the 4th and 8th weeks of the intervention, the female of 1 breeding pair was found dead without prior signs of illness. No cause of death was identified on necropsy. The pair was treated as missing for the eighth and 12th weeks of follow-up, and only 4 wk of breeding data for this pair was tracked during the intervention. Gerbil age by cage was included in the analysis to account for the passage of time during the study. Because the male and female in each breeding pair were within 2 d of age, the median age of the 2 adults was used to calculate their age in months. For data interpretation, a month was defined 30 d for interpretability, such that 12 mo indicates 360 d.

Temporal relationship between digging and jumping. To assess the temporal relationship between baseline stereotypic digging and stereotypic jumping, the 9,118 corner jump events were descriptively categorized based on the relative timing of the 2 behaviors. Jumps that occurred less than or equal to 2 seconds before stereotypic digging were categorized as 'before digging,' and jumps that occurred less than or equal to 2 s after stereotypic digging ended were categorized as 'after digging.' Jumps that occurred within 2 s of a digging interval were categorized as 'between digging,' and jumps that occurred during the digging bout were categorized as 'during digging.' All other jumps were categorized as 'not associated with digging.'

Effect of the intervention on duration of stereotypic digging. To assess the relationship between the intervention and the duration of stereotypic digging, a mixed effect modeling approach was used to account for the repeated measurements over time. Given that individual gerbil pairs could have different baseline behavior, random intercepts were employed to allow for correlation among pairs. Due to the nonnormal distribution of dig duration, a log transformation was used to satisfy model assumptions. As sequential measurements on gerbils are correlated over time, a spatial power structure was used. This structure assumes that measurements closer in time are more strongly related.[28] As the age of adult gerbils was thought to be related to the outcome, it was also included in the model.

Effect of the intervention on stereotypic digging and jumping counts. Similar to dig duration analysis, the association between the intervention and the number of stereotypic digging bouts was fit using a mixed effect modeling approach that controlled for age. Once again, random intercepts and a spatial power structure were applied to account for correlation over time and within gerbil pairs. A negative binomial generalized mixed model was used to account for the large number of observations in which no stereotypic behaviors were recorded.[28] This analysis was repeated using the number of stereotypic jumps as the outcome of interest. To assess the impact of stereotypic behavior over time, all previous models were repeated substituting 'week' for 'intervention.'

Stereotyped behaviors and tube shape. Descriptive statistics were used to assess the association between the intervention tube shape and stereotypic digging or jumping. The 4 tube shapes were: Straight, L, T, and XYZ.

Breeding analysis. Analysis of the association between the intervention and the number of pups born and weaned, controlling for age, used the same mixed effect modeling approach as used to assess the number of stereotypic digging bouts and jumping events. Because the length of the baseline period differed from observation periods, an offset was used in the model to account for this discrepancy. The offset removes the possibility that a difference in number of pups weaned is attributable to length of time.

Data cleaning, descriptive statistics, data visualization, and power calculations were determined using R version 4.0.2 (R Foundation for Statistical Computing). Regression models were carried out in SAS version 9.4 (SAS Institute).

Results

Characterization of corner jumping and digging stereotypic behaviors. All pairs engaged in stereotypic corner digging during the baseline period. During this initial observation period, 16 of 17 (94%) gerbil breeding pairs were observed corner jumping during 1 or more of the 3 daily 30-min observation periods. Gerbil stereotypic activity was highest during the PM observation period as compared with the Noon and AM observation periods. The PM period had 272 corner digging bouts as compared with 44 Noon and 26 AM corner digging bouts. The median corner dig duration was (14.5 s) during the PM period as compared with the Noon (8.8 s) and AM (11.6 s) periods. The number of jumps was also (1604) during the PM period as compared with the Noon (240) and AM (250) periods (Table 1). The incidence of productive (nonstereotypic) digging behaviors during the baseline week was too low for meaningful analysis. Based on these data, the PM observation window was selected for baseline data and comparison between intervention and tube type conditions.

Over half (61.1%) of the stereotypic jumps observed during the baseline period occurred during a bout of stereotypic digging. In these cases, gerbils would briefly pause their forelimb digging motions, and while still standing only on their rear legs, would jump vertically toward the cage lid repeatedly, then resume forelimb ± hindlimb corner digging motions. Nearly one-third (30.6%) of observed jumps happened more than 2 s before or after a digging bout and were therefore not considered to be associated with digging. The remaining jumps occurred before digging (7.3%), between digging periods (0.3%), and after digging (0.6%) (Table 2).

Descriptive statistics. The data were highly right-skewed, so medians were used for data analysis instead of means. The median duration of stereotypic digging bouts was 13.9 s (interquartile range (IQR), 5.2 to 36.8) during the baseline period and 17.0 s (IQR: 6.6 to 46.6) during the 12-wk intervention.

Table 2. Stereotypic corner jumping in temporal relation to stereotypic corner digging.

Temporal Period	Overall (n = 9,118)
After Digging	58 (0.6%)
Before Digging	668 (7.3%)
Between Digging	30 (0.3%)
During Digging	5,574 (61.1%)
Not Associated	2,788 (30.6%)

Table 3. Descriptive statistics of stereotypic behaviors and breeding by gerbil pair over time.

		Intervention Period				Overall
	Baseline	Week 01	Week 04	Week 08	Week 12	Intervention
Dig Length (Sec)	(*n* = 354)	(*n* = 551)	(*n* = 278)	(*n* = 474)	(*n* = 479)	(*n* = 1882)
Mean (SD)	32.8 (47.1)	38.4 (49.0)	38.8 (45.3)	39.7 (51.5)	33.9 (48.7)	37.4 (49.1)
Med (Q1, Q3)	13.9 (5.2, 36.8)	17.5 (7.4, 46.5)	20.7 (8.3, 52.2)	17.5 (6.5, 53.8)	14.3 (5.9, 38.2)	17.0 (6.6, 46.6)
Initiated Digs	(*n* = 102)	(*n* = 119)	(*n* = 119)	(*n* = 112)	(*n* = 112)	(*n* = 462)
Mean (SD)	3.5 (5.9)	4.6 (6.3)	2.3 (3.6)	4.2 (4.5)	5.2 (7.8)	4.1 (5.8)
Med (Q1, Q3)	1.0 (0, 5.0)	2.0 (0, 6.0)	1.0 (0, 3.0)	3.0 (0, 7.0)	2.0 (0, 7.0)	2.0 (0, 6.0)
Total Daily Dig Duration (Sec)						
Mean (SD)	113.9 (233.7)	177.9 (279.5)	90.7 (159.1)	167.8 (248.7)	167.0 (256.5)	150.4 (241.8)
Med (Q1, Q3)	4.6 (0, 123.5)	28.9 (0, 273.6)	5.2 (0, 123.1)	53.1 (0, 239.5)	31.6 (0, 232.0)	23.6 (0, 206.9)
Jumps						
Mean (SD)	17.8 (36.6)	19.3 (37.8)	13.3 (30.9)	15.4 (25.5)	15.1 (30.5)	15.8 (31.5)
Med (Q1, Q3)	0.0 (0, 15.2)	3.0 (0, 19.0)	1.0 (0, 14.5)	4.5 (0, 20.2)	0.0 (0, 17.2)	3.0 (0, 18.0)

Summary statistics from the primary analysis are presented by week. The Overall Intervention column presents summary statistics across all intervention weeks. Dig Length is the corner dig duration in seconds per bout. Initiated Digs are the number of digging bouts by a gerbil pair per daily 30-min observation period, and Total Daily Dig Duration is the total daily duration of all digging bouts by a gerbil pair. Jumps is the number of jump events per gerbil pair during the daily 30-min observation period.
N represents the number of observations. Dig Length observations are the number of bouts that occurred across all gerbils during each time period. Observations are at the gerbil pair-day level for Initiated Digs, Total Daily Dig Duration, and Jumps, such that one day of complete data has 17 observations.

Because only a subset of gerbil pairs engaged in stereotypic digging during a given observation period, the median digging duration for the 30-min daily observation period was 4.6 s (IQR: 0 to 123.5) during the baseline period and 23.6 s (IQR: 0 to 206.9) during the intervention. The median number of digs per daily 30-min observation period was 1 (IQR: 1 to 5) during the baseline period and 2 (IQR: 0 to 6) during the intervention. In contrast, the median number of jumps recorded for each day was lower during the intervention (Med: 3, IQR: 0 to 18) than baseline (Med: 0, IQR: 0 to 15.2) (Table 3).

At least 1 gerbil pair did not engage in one or both stereotypic behaviors in 398 30-min observation periods. In more than half (52%) of these observations, neither digging nor jumping occurred. Only 7 (2%) observations had jumping without digging and 46% of observations had digging without jumping.

Stereotypic digging duration. On average, the duration of stereotypic digging per bout was 25% longer (95% CI: 9% to 44%) during the intervention than baseline, after controlling for the median age of the breeding pair ($P = 0.002$). Specifically, the average digging duration was 26% longer (95% CI: 7% to 48%) during Week 1 as compared with baseline ($P = 0.005$), 32% longer (95% CI: 9% to 59%) in Week 4 compared with baseline ($P = 0.004$), and 28% longer (95% CI: 8% to 51%) in Week 8 than baseline ($P = 0.004$). The digging duration in week 12 was not significantly different from baseline ($P = 0.098$) (Table 4).

Age was also associated with the length of stereotypic digging bouts by each gerbil pair. The median age of the gerbil pairs during the baseline period was 14.9 mo (IQR: 6.7 to 18.0) during the baseline period and 15.8 mo (IQR: 7.7 to 19.4) during the intervention period. Every increase in gerbil age by 30 d was associated with a 2% decrease (95% CI: 0.34 to 4) in the average dig duration ($P = 0.022$) (Table 4).

Incidence of stereotypic digging. The addition of opaque enrichment tubes did not significantly alter the number of stereotypic corner digging bouts per 30-min observation period. The intervention period had 29% more (95% CI: 8% less to 81% more) initiated digs per 30-min daily observation period compared with baseline, after adjusting for the median age of the breeding pair ($P = 0.146$). Specifically, no significant differences were detected in the number of initiated stereotypic digs between baseline and Week 1 ($P = 0.101$), Week 4 ($P = 0.136$), and Week 8 ($P = 0.118$). However, week 12 had a 1.8 (95% CI: 1.2 to 2.7) fold increase in the average number of digs per observation period; this was significantly different from baseline ($P = 0.005$) (Table 4).

Age was significantly associated with the number of digs initiated per observation period. A month increase in the median age of the breeding pairs was associated with a 5.5% decrease (95% CI: 1.9% to 9.0%) in the number of corner digging bouts recorded ($P = 0.004$) (Table 4).

Incidence of stereotypic jumping. The enrichment tube intervention was not significantly associated with the number of stereotypic jumps per 30-min daily observation period, after controlling for age ($P = 0.713$). All weekly comparisons were also nonsignificant. Age had a significant negative association with the number of jumps; a 1 mo increase in the median age of the breeding pair was associated with a 7.5% decrease (95% CI: 1.3% to 13.3% decrease) in the number of jumps per observation period ($P = 0.020$) (Table 4).

Three breeding pairs had fewer than 100 recorded stereotypic jumps during the study period, while 2 cages had 1,110 and 2,143 jumps respectively during the same interval. These 2 'high jumping' cages also had the most time spent engaging in stereotypic corner digging during the entire observation period. These breeders engaged in 192 and 221 min of corner digging, respectively, during 1,020 min of recorded PM observations for each cage.

Exploratory assessment of tube shape. The intervention was analyzed after subdivision by tube shape (Table 5) Each tube shape group (S, L, T, XYZ) had large variation within the group for all outcomes (Figure 3, Table 5). For example, the average number of weekly jumps per gerbil pair in the L, S, and XYZ groups was respectively 16.2 (range: 1.5 to 49.0), 23.5 (range: 5.8 to 55.7), and 14.1 (range: 0 to 51.8) during baseline and 12.6 (range: 0.3 to 62.6), 28.5 (range: 4.4 to 90.6) and 15.6 (range: 0 to 55.7) during the intervention. The mean number of jumps in the T tube group was 18.1 at baseline (range: 1.5 to 59.7) and 6.6 (range: 0.9 to 16.1) during the intervention, generating a

Table 4. Impact of the intervention on stereotypic behavior duration and incidence.

Stereotypic Corner Dig Duration					
Intervention			Week		
Parameter	Estimate	*P*	Parameter	Estimate	*P*
Intervention	1.253 (1.09,1.442)	0.002	Wk1	1.258 (1.071,1.479)	0.005
Age	0.976 (0.956,0.997)	0.022	Wk4	1.321 (1.094,1.595)	0.004
			Wk8	1.28 (1.082,1.515)	0.004
			Wk12	1.157 (0.973,1.375)	0.098
			Age	0.981 (0.959,1.003)	0.092
Number of Stereotypic Corner Digs					
Intervention			Week		
Parameter	Estimate	*P*	Parameter	Estimate	*P*
Intervention	1.288 (0.916,1.809)	0.146	Wk1	1.385 (0.939,2.043)	0.101
Age	0.945 (0.91,0.981)	0.004	Wk4	0.729 (0.482,1.103)	0.136
			Wk8	1.382 (0.922,2.072)	0.118
			Wk12	1.806 (1.201,2.717)	0.005
			Age	0.934 (0.9,0.97)	<0.001
Number of Stereotypic Corner Jumps					
Intervention			Week		
Parameter	Estimate	*P*	Parameter	Estimate	*P*
Intervention	1.076 (0.729,1.587)	0.713	Wk1	1.131 (0.714,1.792)	0.6
Age	0.925 (0.867,0.987)	0.02	Wk4	0.875 (0.549,1.394)	0.575
			Wk8	1.087 (0.669,1.765)	0.737
			Wk12	1.281 (0.773,2.124)	0.337
			Age	0.916 (0.854,0.983)	0.015

Effects of the intervention on primary outcomes. The Intervention column presents the effect of adding enrichment tubes across all time points and the Week column presents the effects of specific weeks of the intervention. Estimates above 1 indicate a positive association with the outcome and estimates below 1 indicate a negative association with the outcome. Baseline is the reference level for all comparisons. Age is reported as the median continuous age of each gerbil pair in months, where a month was defined as 30 d. Intercept terms are not reported. $P \leq 0.05$ is considered significant.

future hypothesis that there may be an association between the T tube shape and decreased corner jumping behavior. The mean number of digs and median dig duration also varied widely among gerbil pairs in all of the tube shape groups during both the baseline and intervention periods (Table 5). Some pairs in the L, T, and XYZ groups were observed corner digging less than once per week on average, while other gerbil pairs had an average of over 10 weekly digging events during baseline (S: max 10.5) or the intervention (L: max 13.6, S: max 15.3, XYZ: max 10.7) (Table 5). Breeding success for the gerbil pairs also varied within each tube shape group during the intervention and control periods (Table 5).

Durability of enrichment tubes. Although not a formal goal of this study, opaque enrichment tubes were monitored for excessive chewing and sharp edges during regular health check assessments. Throughout the 12-wk intervention period, 3 gerbil pairs required tube replacement because of chewing, and 1 of these pairs required 2 sets of replacement tubes (3 sets total) due to continued chewing. Tubes were not noticeably deformed by sanitation in cagewash.

Breeding performance. The number of pups weaned per breeder pair was similar during the control periods (median: 0, IQR: 0 to 4.7 pups weaned per 30 d) and the intervention (median: 0.3, IQR: 0 to 4.5 pups weaned per 30 d), without adjusting for age (Table 6). A significant association was detected between the age at the start of each observation period and the number of pups weaned. Each 30-d increase in the median age of the breeding pair was associated with a 23% decrease (95% CI: 17 to 28) in the number of pups weaned per observation period ($P < 0.001$). The use of opaque tube enrichment was not associated with a significant change in the number of pups weaned, after adjusting for age ($P = 0.422$) (Table 7).

Discussion

We used a noninvasive method of observing breeding gerbils in their home cages to characterize the incidence and duration of stereotypic corner digging and jumping behaviors. The gerbils engaged in the most stereotypies during the 30 min period just before the beginning of the dark phase. Adding opaque PVC tubes as tunnel-like enrichment was associated with a greater duration of stereotypic corner digging behavior for the duration of the 12-wk study. The incidence of corner jumping behaviors was not significantly affected by the presence of opaque tubing in the cage (Table 4).

The frequency and duration of observed stereotypic behaviors varied greatly between gerbil breeding pairs (Figure 3, Table 5). Although gerbils in all cages were recorded engaging in stereotypic corner digging and corner jumping over the course of the study, some cages accounted for significantly more of these behaviors than others. This could suggest that corner digging and corner jumping as stereotypic behaviors are closely related, potentially by sharing a similar motivation or environmental trigger to initiate the behavior. An alternative hypothesis is that certain individuals are more likely to engage in stereotypic behaviors. The results of this study could support the idea that the 2 behaviors have different causes or motivations, because stereotypic digging

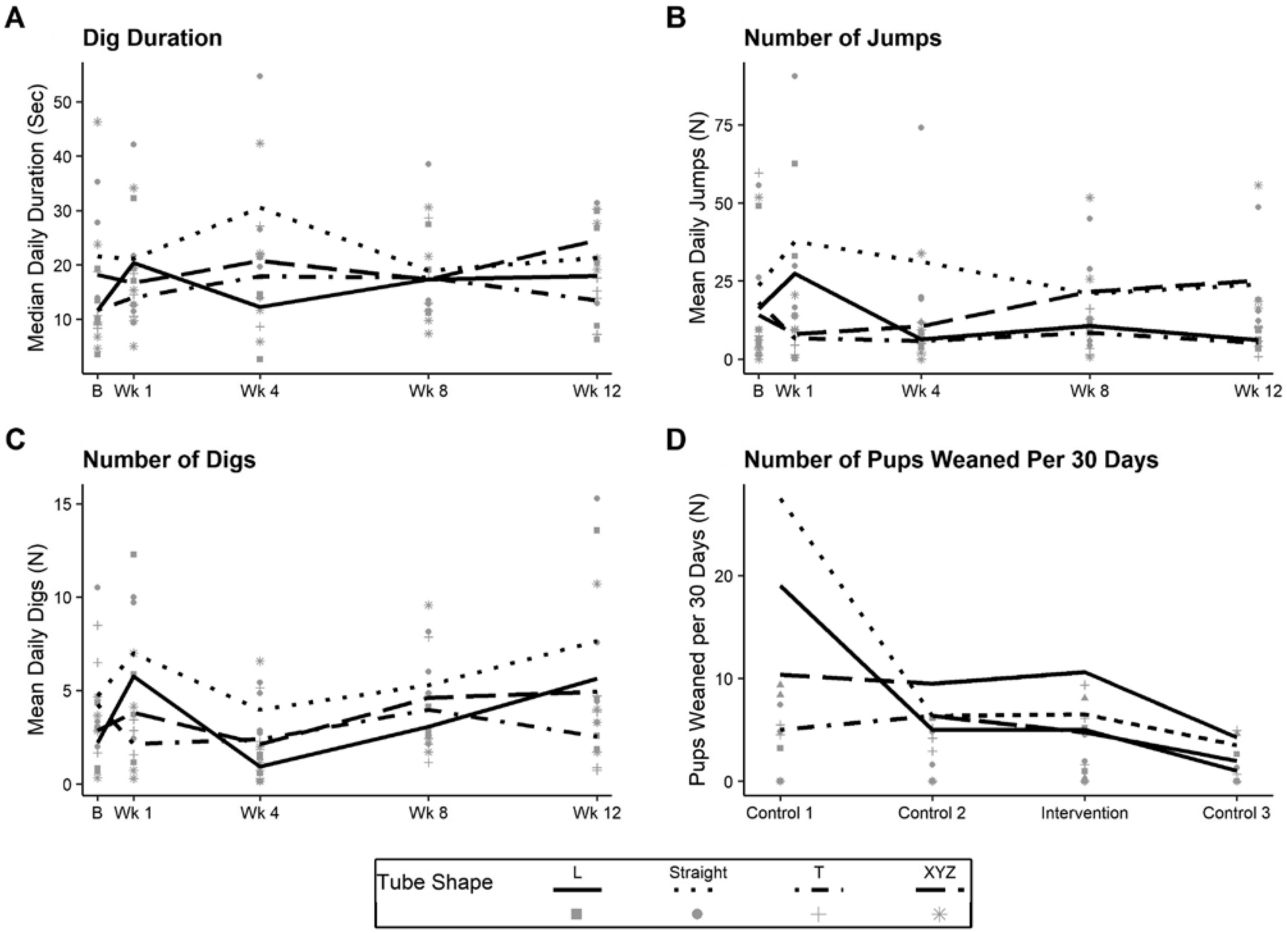

Figure 3. Individual and averaged trajectories of each stereotypic behavior by tube shape over time. (A) median corner dig duration, (B) mean number of corner jumps, (C) mean number of corner digging bouts, and (D) number of pups weaned. Because of highly influential outliers, dig duration is expressed in terms of the median daily dig duration by gerbil pair in seconds. The number of pups weaned is the total number of pups weaned by gerbil pair per 30 d. B is an abbreviation for baseline, and all week time points are during the intervention. In many cases, one gerbil pair greatly alters the overall average for the tube group. This figure does not incorporate age as a variable.

Table 5. Association of tube shape with stereotypic behaviors and breeding efficiency.

	Tube Shape			
	L	Straight	T	XYZ
Median Dig Duration				
Baseline	11.6 (3.5, 19.4)	21.6 (9.3, 35.3)	11.7 (8.4, 18.8)	18.2 (4.6, 46.3)
Intervention	17.0 (2.7, 32.2)	23.0 (8.3, 52.2)	15.8 (6.5, 53.8)	19.7 (5.9, 38.2)
Mean Number of Digs				
Baseline	2.2 (0.7, 4.3)	4.7 (2.0, 10.5)	4.2 (0.3, 8.5)	2.9 (0.3, 4.7)
Intervention	3.8 (0.1, 13.6)	6.0 (2.1, 15.3)	2.8 (0.3, 7.9)	3.8 (0.1, 10.7)
Mean Number of Jumps				
Baseline	16.2 (1.5, 49.0)	23.5 (5.8, 55.7)	18.1 (1.5, 59.7)	14.1 (0, 51.8)
Intervention	12.6 (0.3, 62.6)	28.5 (4.4, 90.6)	6.6 (0.9, 16.1)	15.6 (0, 55.7)
N Weaned/30 Days				
Control	2.0 (0, 7.4)	3.2 (0, 9.4)	1.3 (0, 6.1)	2.5 (0, 4.5)
Intervention	1.6 (0, 4.5)	2.1 (0, 8.1)	1.5 (0, 5.2)	3.4 (0, 9.4)

The median dig bout duration, mean number of dig events, mean number of jump events, and number of pups weaned per 3-mo observation period are presented by tube shape and observation period. All statistics report the mean and range. For example, dig duration observations were calculated as the median dig duration per gerbil pair per week. The mean and range of these observations is presented by tube shape. N Weaned/30 days presents the number of pups weaned per 30-d interval to account for differences in the lengths of the breeding observation periods.

generally increased during the intervention, while jumping behavior was statistically unchanged (Table 4). Additional research will be needed to define the relationship between the motivations for stereotypic corner digging and corner jumping and whether the same intervention can effectively address both behaviors.

Table 6. Breeding performance summary statistics.

	Control 1 (n = 9)	Control 2 (n = 14)	Intervention (n = 17)	Control 3 (n = 16)
n Born/30 d				
Mean (SD)	5.5 (3.5)	2.8 (3.2)	3.0 (3.3)	1.2 (1.8)
Median (Q1, Q3)	5.8 (4.8, 7.7)	1.3 (0, 6.0)	2.3 (0, 5.4)	0.0 (0, 1.9)
n Weaned/30 d				
Mean (SD)	4.8 (3.3)	2.2 (2.6)	2.2 (3.2)	0.9 (1.7)
Median (Q1, Q3)	4.8 (3.2, 7.4)	0.8 (0, 4.7)	0.3 (0, 4.5)	0.0 (0, 0.8)
Age (Months)				
Mean (SD)	6.0 (1.9)	11.0 (4.9)	13.3 (6.0)	16.0 (6.1)
Median (Q1, Q3)	6.2 (5.3, 7.4)	12.3 (9.7, 14.2)	15.2 (6.9, 18.3)	17.6 (10.0, 21.4)

Control 1 occurred from November 21, 2018 to February 21, 2019; Control 2 occurred from July 21, 2019 to October 21, 2019; the opaque tube intervention period was from November 21, 2019 to February 21, 2020; and Control 3 occurred from February 22, 2020 to May 22, 2020. During Control 1, only 9 of the gerbil pairs that would participate in the Intervention had been paired. By Control 2, 14 of the Intervention pairs had been paired for breeding. During Control 3, 16 of the Intervention pairs remained together for breeding. N Born and N Weaned are reported in terms of the number of pups born or weaned per 30 d. Age is reported as the median age in months (30 d) by gerbil pair at the start of each observation period.

Table 7. Effect of intervention and breeding pair age on number of pups weaned.

Parameter	Estimate	*P* value
Intervention	1.36 (0.647, 2.862)	0.422
Pair Age	0.773 (0.720,0.829)	<0.001

Findings from the analysis of the effects of the intervention and age on the number of pups weaned per observation period. Age is reported as the median age of the gerbil pair at the start of each period in months, where a month was defined as 30 d. Estimates above 1 indicate a positive association with the number of pups weaned and estimates below 1 indicate a negative association with the number of pups weaned. Each monthly increase in the median age of the breeding pair was associated with a 23% decrease (95% CI: 17 to 28) in the number of pups weaned per observation period ($P < 0.001$). The intervention was not significantly associated with the number of pups weaned ($P = 0.422$).

Although the addition of enrichment tubes was intended to decrease incidence and duration of stereotypic behaviors, we observed an increase in corner digging duration that persisted for at least 8 wk after tube placement. Although corner digging duration was not significantly increased during week 12, a significant increase in the number of corner digging bouts did occur during that week (Table 4). Initially, we considered whether this increase in stereotypic behavior could be a result of neophobia, as has been described in other rodents as well as nonhuman primates and psittacines.[10,20,31,32] However, we would not have expected neophobia to play a major role after the gerbils had been living with the same enrichment for multiple months as in this study. The addition of opaque enrichment tubes in the cages could have been a source of chronic stress that could have led to more stereotypy in the gerbils. Although we noted no other macro- or microenvironmental changes during the study period, the gerbils could have experienced other, unidentified stressors during the intervention period. In future work, comparing fecal corticosterone levels could gauge the effects of undefined stressors and enrichment interventions on physiologic stress.[27,37] Our results do not support the hypothesis that the simple addition of enrichment tubing would lead to an eventual decrease in stereotypic behaviors.

Time was a confounding factor in the study design. We attempted to address this by incorporating age into the statistical analysis models for stereotypic behaviors and breeding. However, including a period of behavioral observation after the opaque enrichment tubing was removed from the cages (an ABA' design) would have been an alternative strategy.

Our study showed that older gerbils spent less time engaged in stereotypic behaviors (Table 4). In other animal species and in humans, stereotypies can be self-reinforcing and may be performed more often over time.[1,18] We expected to find this situation in the gerbil breeding colony. However, the stereotypic behaviors that we assessed are possibly more physically taxing than those reported in these other species, and gerbils may simply perform them less as they age and their overall activity levels decrease.

The timing of our intervention may have limited its effectiveness in reducing incidence of stereotypies in breeding gerbils, as they were adults when the study began. Some studies have reported that as animals age, stereotypic behaviors become less likely to respond to enrichment.[9,21] However, the literature is not unanimous on this point.[13,14,22] As wild-caught animals of multiple species are less likely to develop stereotypies, a critical period may occur early in life when provision of appropriate enrichment can maximally protect against the development of stereotypies.[6,9] Some data support this idea in gerbils specifically; young gerbils raised without a burrow display intensified stereotypic digging behavior.[36] More studies would be needed to define the developmental stages during which additional enrichment could be maximally effective in preventing stereotypic behavior.

Although we anticipated that we did not test enough breeding cages to power a definitive comparison between different enrichment tube shapes, we chose to pilot-test 4 different shapes for differences in their potential effects on gerbil behavior and to allow the husbandry staff to provide feedback on which, if any, were preferred by caretakers or gerbils. Gerbil care staff provided informal, verbal feedback on the use of enrichment tubes, including both practical considerations and a perceived preference by the animals. Each tube shape had theoretical pros and cons (summarized in Figure 1). The Straight tube provided the best view of the animals for animal care staff, but did not create a realistic, angled entrance into the gerbils' simulated burrow. The L tube shape was more similar to published enrichment strategies associated with a decrease in stereotypic behavior in gerbils.[29] The T tube provided a better view of the animals for animal husbandry staff, but we speculated that its comparatively open shape could reduce the gerbils' sense of an enclosed, safe place. The XYZ tube created a more 3-dimensional experience for the gerbils, allowing them to come 'up' from their artificial burrow. Throughout the intervention period, gerbils with XYZ tubes were recorded using the vertical opening to periscope and survey their surroundings. Caretakers' ability to visualize the gerbils with XYZ tubes was reported as poor, as were the L tube groups. Although the gerbil caretakers were not formally surveyed about their tube shape preferences, several caretakers expressed appreciation for the ability of the XYZ tubes to promote species-specific behavior by mimicking emergence from an underground passage.

Larger group sizes would be needed to adequately power a study comparing the association of stereotypic behaviors with different opaque tube shapes, given the variability in behavioral data that we observed among the pairs. Using the data collected in this study, achieving 80% power, an observed effect size of 0.39, no covariate adjustments, and 5% attrition from the study would require 111 breeding gerbil pairs per group to make 1 comparison in the incidence of stereotypic behavior expression by a gerbil pair, with or without tube enrichment, using an independent 2-sample *t* test. This number far exceeds our institution's gerbil breeding colony size.

Overall, the addition of enrichment tubes was not associated with a statistically significant change in corner jumping behavior (Table 4). When the individual tube shape was considered, gerbils with T tubes had the lowest number of jumps throughout the enrichment observation period (Table 5). However, future studies with larger group sizes would be needed to determine if this is a true effect of the tube shape or an artifact related to inadequate group sizes. With group sizes of 4 to 5 cages, one gerbil pair may greatly alter the mean of the tube shape group, as seen in Figure 3.

We anticipated that gerbils with the highest incidence of stereotypic behaviors would have the lowest breeding success. However, stereotypic behaviors did not appear to correlate with breeding success or failure. The 5 breeding pairs with the fewest jumps and least time spent digging had zero pups weaned during the intervention study. Unexpectedly, 1 breeder pair with the second-highest number of jumps and the most time spent corner digging weaned 29 pups during the same period, the most of all breeding pairs. Conversely, the breeding pair with the highest number of jumps and second-most time spent corner digging weaned no pups during the 3-mo study. Thus, the relationship between frequency or duration of stereotypic behaviors and breeding success during the same period is not clear. However, we found that the number of pups born and weaned decreased with gerbil age (Table 6, Table 7).

Interpretation of the breeding data compared with the prior year may have been complicated by a nearby construction project, which began in late January 2019 and continued past the end of the study period. For this reason, we also compared the study breeding data to the previous 3 mo, although this comparison could be affected by seasonal variation. The study was conducted during the fall and winter months, which are anecdotally associated with lower breeding success as compared with the summer months. By looking at breeding data immediately following the intervention, we were able to confirm that age was more likely to account for observed decreases in fecundity than the enrichment intervention itself.

Because we were interested in testing different tube types, the attachment between the opaque nest boxes and the enrichment tubes was not made permanent. This allowed the gerbils to move the opaque tubes from the nest box entrance to other areas in the cage. This design is different from the artificial burrow previously reported to help reduce gerbil stereotypies, which may have contributed to our results that conflict with this prior work.[29,30] One breeding pair did not move the tube from the burrow entrance during the study, but all other pairs were observed pushing and/or pulling the tubes around the cage, using their teeth and forelimbs. We considered that this autonomy over the layout of their living space would confer an enriching effect, so the tubes were not immediately replaced in the nest box entrance after the gerbils moved them. This also minimized additional disturbance of the breeding cages, which could be expected to negatively impact breeding success. However, our results suggest that the gerbils' ability to move the opaque tubing did not have a significant impact on the incidence of stereotypic behaviors. A permanently attached tunneled-burrow unit could be more effective at reducing gerbil stereotypies as compared with providing the tubes as separate enrichment components.[29,30,35] Without fixing the tubes in place at the entrance to the gerbils' next boxes, we cannot rule out that the effect of the enrichment in our project may have been different if the tubes had a consistent orientation within the cages.

Some breeding pairs used the enrichment tubes as gnawing materials and had to have their tubes replaced throughout the study due to sharp edges or significant damage to the tube. The breeding pair that was given 2 sets of replacement tubes had relatively low rates of stereotypic digging or jumping. However, the low incidence of stereotypic behaviors was probably not due to the availability of the tubes as a preferred chewing substrate because this pair had low levels of stereotypic behaviors at baseline. This pair weaned no pups during the intervention period. Therefore, we cannot draw any conclusions about whether the chewing behaviors were related to their low breeding success.

The incidence of stereotypic behaviors in our breeding gerbil colony, including a novel jumping stereotypy not previously described in gerbils, suggests that additional strategies are needed to address their ethological needs. The provision of a moveable opaque enrichment tube to function as a tunnel-like entrance to a simulated burrow did not significantly reduce stereotyped behaviors or improve breeding success among the gerbil pairs. Instead, the addition of opaque enrichment tubes was associated with an increase in stereotypic digging behavior that did not return to baseline over 12 wk of observation. The unobtrusive behavioral observation strategy developed to measure the effect of additional enrichment in breeding gerbil cages can be easily adapted to other welfare projects within the vivarium.

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