Wageningen University - Department of Animal Science

Spontaneous trial-and-error learning of operating an enrichment device in domestic cats (*Felix catus*).

MSc Thesis

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Abstract

Big cats in captivity often show abnormal repetitive behaviour (ARB), indicating poor welfare. ARB may be caused by frustrated behavioural needs, including hunting behaviour. An enrichment device that facilitates such hunting behaviour could improve the welfare of captive cat species, and the present study contributes to its development. Domestic cats are a good study model for testing out enrichment devices for big cats and here we assessed the learning ability of domestic cats when learning operant behaviour, necessary for operating the enrichment device, by trial-and-error. The enrichment device for stimulating feline hunting behaviour was a reversed vending device that delivered food after cats nudged a ball (the operant) into a receptacle. Sixteen cats had access to the device in a metabolic cage, for 3 minutes at a time, to test for trial-and-error learning of the operant. Initially, the ball was placed such that an accidental touch caused it to roll into the receptacle. A total of 336 trials (each 3 minutes) were recorded, with 53 of those extensively analysed using an ethogram. Logistic regression analyses showed a significant ($p < 0.001$) effect of the trial number on the probability of the ball going in, and thus a learning curve. Linear mixed model analyses showed that the behaviours walking, jumping and meowing (together indicating anxiety) were associated with a decrease in successful ball delivery. Anxiety impaired learning performance, especially in the beginning. This study showed how cats had a learning curve in operating an enrichment device, and they became increasingly relaxed in the test setting. The finding that domestic cats learned to operate this enrichment device by trial-and-error opens the way for using such enrichment devices for bigger cat species in captivity. However, anxiety in cats impaired learning, and novelty-induced anxiety can make that individual (big) cats do not learn to operate the enrichment device and miss out on the benefits from increased play and natural behaviour.

Key words: trial-and-error, learning, cats, anxiety, behaviour, animal welfare, enrichment.

Introduction

Big cat species are adapted to living in large home ranges and spend a significant amount of time on predatory behaviour, which makes it unsurprising that these species do not do well in captivity (Clubb and Mason, 2007). Carnivorous species in zoos commonly show stereotypic behaviour, as shown in a review that summarizes the results of papers on 20 species, with an estimated prevalence of 82% for captive carnivorous species (Mason & Latham, 2004). Stereotypic behaviour is abnormal repetitive behaviour (ARB) indicative of poor welfare caused mainly by frustrated behavioural needs (Mason et al., 2007). When 33 studies were used to calculate the time spent on stereotypic behaviour, it was found that the big cat species in zoos within the genus *Panthera* and *Neofelis* showed a relatively high prevalence, with lions (*Panthera leo*) spending 48% of their time on stereotypic pacing and jaguars (*Panthera onca*) 21% (Clubb & Mason, 2007). Other carnivorous species showed less stereotypic behaviour, with a prevalence of 7% for the snow leopard (*Uncia uncia*) and only 0.2% for the red fox, but in general stereotypic behaviour is a major problem in big cat species in captivity. For practical reasons and ethical considerations, captive big cats are rarely given live prey to feed on and instead get their food already dead and prepared. This prevents big cats from performing their natural hunting behaviour (Szokalski et al., 2012). Combined with the lack of space to roam in, since zoos are often constricted spatially, this leads to frustrated motivations to hunt and/or move (Szokalski et al., 2012). Abnormal repetitive behaviours, such as stereotypic pacing, may be the outcome of this frustration (Riggio et al., 2019). Captive ocelots (*Leopardus pardalis*) showed increased stereotypic pacing during crepuscular hours, the hours during which wild carnivores are normally more active, indicating that such pacing resulted from frustrated appetitive foraging, i.e. hunting (Weller & Bennet, 2001). Stereotypic behaviour can be a 'scar' from a previous living environment, and the lack of stereotypic behaviour is not per definition a sign of good welfare, but typically it indicates impaired welfare. A comprehensive review on several hundred publications on the association between stereotypic behaviour and either good, bad or uncertain welfare showed 68% of the stereotypic behaviours to be associated with reduced welfare (Mason & Latham, 2004). Unnatural time budgets may be a further indication of poor welfare and comparing the behaviour of captive animals versus the behaviour of these animals in the wild is one way to assess animal welfare (Webster, 2005). Other measures of animal welfare, such as corticosteroids, reproductive rates or infant mortality can support valid welfare assessments of carnivorous species in zoos (Clubb and Mason 2007). Findings in these indicate that clearly there is a need for improving the welfare of big cats in captivity.

Stereotypic behaviour may be reduced by enrichment and providing opportunities or choices that were not there before (Swaisgood & Shepherdson, 2005). Environmental enrichment aims to provide species-specific meaningful stimuli that promote psychological well-being (Mellen & Sevenich MacPhee, 2001; Shepherdson et al., 1998). Environmental enrichment is often used to reduce stress in captive animals by meeting their behavioural needs by improving the environment's complexity (Ellis, 2009). Most environmental enrichment for cat species focuses on feeding and hunting practices, since they likely value hunting, given its importance to their fitness in the wild (Szokalski et al., 2012). Enrichment that facilitates hunting behaviour is likely to increase their welfare in captivity. When three novel feeding treatments were introduced to 6 big cat species in zoos (n=14), the stereotypic pacing decreased significantly during two of the treatments (Skibiel et al., 2007). The three treatments were frozen trout, horse bones and a spice blend (cinnamon, chilli powder and cumin) sprinkled on the ground of the enclosure. The stereotypic pacing decreased significantly when provided with frozen trout ($Z = -2.5$, $p = 0.01$) and the spice blend ($Z = -2.67$, $p < 0.01$). With an overall decrease in stereotypic pacing of 21%. Another example of enrichment by feeding practice is when two captive Amur tigers were introduced to feeding boxes that could be manually opened at random (Jenny and Schmid, 2002). The feeding boxes were distributed in the enclosure and filled with meat. The boxes could be opened during random timeslots during the day, thus forcing the tigers to keep investigating the feeding boxes regularly and simulating their natural behaviour of searching for prey. Before the enrichment, the stereotypic pacing was observed to be 16% of their active time. After the feeding boxes were introduced, this decreased significantly to only 1% ($Z = 2.38$, $p = 0.02$). The authors concluded that the pre-observed stereotypic pacing was caused by permanently frustrated appetitive foraging behaviour. Foraging behaviours, including gathering and hunting, can be stimulated through enrichment with a feeding device or feeding practices that make animals acquire their food in a more natural way. Cats could benefit from a reversed vending food delivery device to stimulate their natural hunting behaviour, but they should first learn how to operate it. The learning itself may be part of cognitive enrichment and has the potential to improve animal welfare (Laule et al., 2003).

Training or learning can be framed as environmental enrichment, since it gives back the need of an animal to engage in tasks, such as hunting and foraging as they would do in the wild, and that is obstructed when in captivity (Laule and Desmond, 1998). Animals will voluntarily work for their food, even when that same food is freely available. A way of learning to operate an enrichment device is by trial-and-error, when a certain behaviour or strategy is tried out and rejected when the payoff is lower than alternatives (Young, 2009). Trial-and-error learning means that spontaneous acts are reinforced if as intended and unrewarded if not, eventually creating a learned operant. This training approach is based on positive reinforcement, which contrary to punishment-based training methods, may increase animal welfare, as shown in captive non-human primates (Bloomsmith et al.,

2007) as well as captive jaguars (Garcia et al., 2012). Trial-and-error learning may be a relatively effective training method in (domestic) cats, as compared to e.g. social learning. Cats perform less well in heterospecific social learning, for example from humans (Arahori et al 2023), than dogs do (Topál et al., 2006; Kubinyi et al., 2003). The solitary nature of cats would explain why they are less proficient in social learning than dogs.

The occurrence of ARB behaviour in captive big cats is high, and an enrichment device may help to increase their welfare. However, not much research has been done on learning to use an enrichment device and the effectiveness of spontaneous trial-and-error learning. The working principles of learning to operate a reversed vending enrichment device are tested here with colony living domestic cats. Domestic cats seem to be a good model for big cats as they are from the same family (*Felidae*) and are skilled predators with advanced cognitive abilities (Shajid Pyari et al., 2021; Sherman at al. 2013). The findings of this study provide fundamental knowledge on the learning ability of domestic cats when learning operant behaviour by trial-and-error. The knowledge gained in this pilot study with domestic cats, should support further research on this enrichment device for big cat species in captivity and ultimately improve the welfare of big cats in zoos.

Method

Study population

The study population consisted of 16 cats (8 males and 8 females) from Carus Research Facility of Wageningen University and Research (WUR), the Netherlands. The cats were born either in August or September of 2020, making them one year of age at the time of the study. The cats have previously been in other nutritional and behavioural studies at this facility. At Carus Research Facility, each group (either 8 males or 8 females) was housed in a room of 10.4 m^2, with ventilation and a controlled temperature of 10-17 ºC. The cats had unlimited access to multiple litter boxes and a water bowl, which were cleaned and refreshed daily. During this study, the cats were fed twice a day. In the morning (7 a.m.) they were fed a small portion of kibbles and in the afternoon (5 p.m.) they received the main meal of kibbles and, occasionally, wet food. The smaller portion in the morning was to ensure that the cats would still be motivated for food during experimental trials during the day. They were weighed every week to make sure their weight stayed stable. The cats were socialised and frequently interacted with students and caretakers, making sure that they were used to being handled. The present behavioural study required them to be in a metabolic cage. The cats were used to the metabolic cage, since they were habituated by their caretakers to stay in a metabolic cage as young kittens.

Study design

Cats were observed for spontaneous trial-and-error learning to operate an enrichment device. The device consisted of a reversed vending device that delivered food after cats nudged a ball into a receptacle. The study was performed at the Carus research facility, during an experimental period of 15 weeks (15th November 2021 until the 23rd of February 2022). For the experiment, the cats were placed in a metabolic cage of 0.80 by 1.00 by 0.75 meters. The cage contained the enrichment device, which is designed and provided by Marcus Clauss and created with a 3D printer. The enrichment device was positioned in the centre of the cage and was taped to the floor of the cage, to prevent it from moving. The enrichment device consisted of a ball receiver and a food dispenser (Figure 1). The ball receptacle was placed inside the metabolic cage so that the cat could investigate and engage with it, while the food dispenser was placed outside of the cage, unreachable for the cats. Both the ball receptacle and the food dispenser were connected via a Raspberry Pi. When the ball went into the receptacle (via the hole), a signal was produced to the food dispenser to release a specific amount of kibbles. The rotating compartments of the food dispenser had space for a specific amount of kibbles and released a portion after rotation. The cats were in the metabolic cage for 3 minutes at a time and could operate the enrichment device for a maximum of 3 trials per day, with at least 1.5 hours in between each trial. The cats stayed in the cage for these 3 minutes, regardless of whether or not they put the ball into the receptacle, and thus received kibble. Every trial was filmed using two GoPro's attached to the outside of the cage, to optimize visibility by real-time video recording. The operant that was desired to be learned by the cats was to nudge the ball, which then would roll into the hole of the receptacle because of the declining slope (Figure 1A).

A **B**

Figure 1 (from Marcus Clauss). The enrichment device, created by Marcus Clauss. It consisted of two components; the ball receptacle (A) and food dispenser (B) that were connected by a Raspberry Pi. A) Ball receptacle with the ball on the platform. The platform was not used in this experiment, so the ball was located on the green X mark in the figure at the beginning of each trial. The food dispenser had a declining slope, so the ball would roll in on itself when nudged. B) Food dispenser, made of plastic and created by a 3D printer. It has two levels that rotate (when activated by ball delivery) so kibble would fall out, and to ensure the same amount of food every turn.

Ethical note

This research did not involve animal suffering and efforts were made so the cats would not experience any negative emotions. Operant learning was facilitated by positive reinforcement and the ultimate goal was to help create a device to potentially enrich the lives of (big) cats. The cats needed to be motivated for food and, therefore, were fed a smaller amount than usual in the morning. The cats did not show any signs of distress or anxiety because of the delayed feeding of the daily ration and the cats got their main (big) meal of the day in the afternoon. The cats were habituated to stay in the metabolic cage and were in the cage for no longer than 3 minutes at a time during this study. Cats that showed signs of distress, such as continuously meowing, or continuously scratching the cage, were returned to their own room and if this behaviour occurred at 3 subsequent trials, the cat was not used for further trials.

Data collection

Live observations were performed on cats successfully nudging the ball in the receptacle, resulting in binary data with successful ball deliveries. The cats' detailed behaviours were scored from video footage using an ethogram based initially on a study of Stanton et al (2015) who standardized an ethogram for species within the family *Felidae*. Pilot trials were performed and watched back to adjust the ethogram to this research based on what behaviours our cats performed. The final ethogram used had a total of 27 behaviours (see Table 1). For practical reasons, the full observations were done for a selection of the trials (the 1st, 10th, 15th and 25th trial of each cat). Most trials resulted in a 3-minute-long video, with some trials terminated prematurely. When cats showed unwanted (unruly) behaviours during trials, and if this behaviour occurred for longer than 20 consecutive seconds or 3 times, the trial was immediately terminated. Cats with 3 consecutive trials that terminated prematurely, were eliminated from the study, but the data on these cats were used until the point of elimination. BORIS (Behavioral Observation Research Interactive Software) (Friard & Gamba, 2016) software was used for scoring the behaviours and typically a video was watched three times, to tally all behaviours. First by ear position, then by tail position and then the locomotive states plus other behaviours (see Table 1). The BORIS Synthetic Time Budget feature was used to calculate the durations of behavioural states and the number of occurrences of point events (see Appendix V).

Table 1. The ethogram used to tally and record the 27 behaviours of the cats (n=16) that were observed for 3-minute trials. Here they could spontaneous learn to operate an enrichment device by nudging a ball into a receptacle for a food reward. Most behaviours were timed in seconds, and some behaviours were tallied in rate per minute (rpm). When these behaviours were continuous, it was tallied every 3 seconds.

GROUP	BEHAVIOUR	EXPLANATION
EARS POSITION	Ears neutral	Ears in a neutral, relaxed position
	Ears back	Both ears backwards
	Ears asymmetrical (rpm)	Both ears in a different direction
	Ears flat	Both ears in a forward, flat position
	Ears invisible	At least one of the ears not visible so unable to tally for the position
TAIL POSITION	Tail upright	Tail in an upright position
	Tail down	Tail in, for most cats, neutral position down
	Tail quiver (rpm)	Tail makes rapid movement (tip of the tail mostly)
	Tail invisible	Tail not visible so unable to tally for position
MOTORIC STATES	Walking	Cat walks at a moderate pace
	Standing	Cat stands in same position while on all four feet
	Sitting	Cat sits down with their butt touching the floor and front paws stretched.
	Laying with head up	Cat lies down in a horizontal position with their belly touching on the floor. Their head is upright
	Laying with head down	Cat lies down in a horizontal position with their belly touching on the floor. Their head is down and touching the floor
	Laying none (normal)	Cat lies down in a horizontal position with their belly touching on the floor.
	Out of Sight	The full cat is not visible.
OTHERS	Eating (rpm)	Cat is chewing kibble
	Grooming (rpm)	Cat cleans themselves by licking or chewing on their fur
	Jumping (rpm)	Cat jumps from one level to the other (either up or down).
	Licking (rpm)	Cat licks any surface other than themselves.
	Meowing (rpm)	Cat makes a meowing noise, with no differentiating between different meows. Growls/purrs/hissing are not part of this.
	Rubbing (rpm)	Cat rubs itself on a surface other than the device.

	Nudge the ball with nose (rpm)	Cat touches the ball with their nose
	Nudge the ball with paw (rpm)	Cat touches the ball with their paw
	Paw through opening (rpm)	Cat put their paw through the opening of the device (regardless of the device being activated)
	Interact with ball by playing	Cat plays with the ball, visible by chasing it after shoving it away
	Interact with ball by biting	Cat bites the ball
	Interact with device by sniffing	Cat is sniffing device
	Interact with device by rubbing	Cat is rubbing itself on the device
	Interact with food dispenser	Cat is putting their paws outside of the cage and is touching the food dispenser or tries to bite the cage lining where the food dispenser is attached

Statistical analysis

Behaviours scores were analysed with a principal component analysis (PCA) and linear mixed models (LMM). Binary data were analysed with logistic regression models and nonparametric data were analysed by Spearman Rank correlations and Chi-squares. The PCA was performed to test for associations between the 21 different behaviours, as rare behaviours were excluded from analyses. Fifty-three records on 16 cats were analysed stepwise by omitting behaviours with loadings < $|0.4|$ in the main components. The PCAs were done as described by Herwijnen *et al.* (2018), based on correlation matrices with unrotated components. Principal components represented direction by eigenvectors and scaling by eigenvalues, with loadings calculated as eigenvectors multiplied by the square root of eigenvalues. Component scores integrated original behaviour scores by using loadings as weighing factors. The cut-off percentage for considering components meaningful was an explained variance of ≥ 11%. A Linear Mixed Model (LMM) was performed on the fixed effects of trial number, ball score (if the ball went into the hole or not), and the two-way interaction of trial number and ball score. Trial number was fitted as covariate and the random component Cat accounted for repeated measures on the same experimental unit. The response variates (dependent variables) were the behavioural parameters, including PCA component scores. The data set consisted of 53 records on 16 cats and the used statistical model was as follows:

$$Y_{uvw} = u + Trial\_number_u + Ball_v + Trial\_number_u . Ball_v + Cat_w + e_{uvw}$$

A Logistic Regression (LR) was used to investigate the association between trial number as a covariate and the binary ball score (delivered yes or no) or paw use, i.e. whether or not a cat pawed the receptacle hole. This to investigate the ability of the cats to learn. The data set consisted of 336 records on 16 cats. Spearman Rank correlations were performed to link the current test results to earlier behaviour test outcomes on the personalities of the cats. A Chi-square test on counts was performed to test if sex had an influence on the likelihood of cats delivering the ball. The statistical analyses were performed on GenStat statistical software. P-values below 0.05 were considered statistically significant.

Results

Colony living laboratory cats were observed for trial-and-error learning to operate an enrichment device, with the deposit of a ball in a receptacle resulting in the delivery of kibbles by a food dispenser. Sixteen cats were included in the study, 8 cats were eliminated at a certain stage of the study due to unruly behaviour (frequent meowing, trying to reach the kibble by trying to claw at the food dispenser with their paws outside the cage) or by putting their paw in the ball receiver (instead of the ball) and thus activating the food dispenser (Appendix I). Cats that showed unwanted behaviours, and were removed from the study, were up until that point unsuccessful in delivering the ball. One male cat never got the ball in, but was not removed from the study. Data on successfully depositing the ball in the receptacle consisted of 336 records (trials). Of the 336 trials, 77 were successful; meaning the cat managed to nudge the ball into the hole. Ten of the 16 cats managed to put the ball in the receptacle at least once. The overall success rate was 19.9% ±18.5. Figure 3 shows the success rate per trial number.

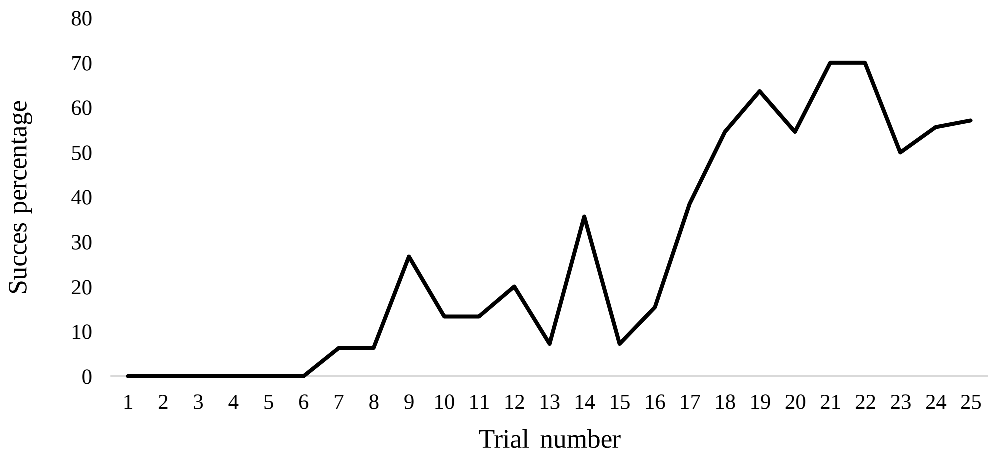

Figure 3. The average success (ball delivery) percentages across trials for 16 cats. Cats (n = 16) were observed for spontaneous trial-and-error learning to operate an enrichment device that delivered food after cats nudged a ball into a receptacle.

The learning process of cats

Ball delivery was expressed binary and 336 records on 16 cats were analysed (logistic regression) for the association between trial number, ranged 1 to 25, and likelihood of cats delivering the ball in the receptacle. The probability of a cat rolling the ball into the receptacle had a predicted mean of 0.15 (± 0.02) and the likelihood increased ($p < 0.001$) as the trials went on (Figure 4). An additional logistic regression was performed with the response variate paw, meaning whether the cats put their paw (instead of the ball) in the hole to receive the food reward. This gave an overall predicted mean of 0.14 (±0.02) and the predicted probability of the paw going into the hole increased significantly ($p < 0.001$) with trial number (Figure 4). However, this time effect was underestimated by the removal of cats not complying to the study design. See Appendix II for the predicted mean scores per individual cat.

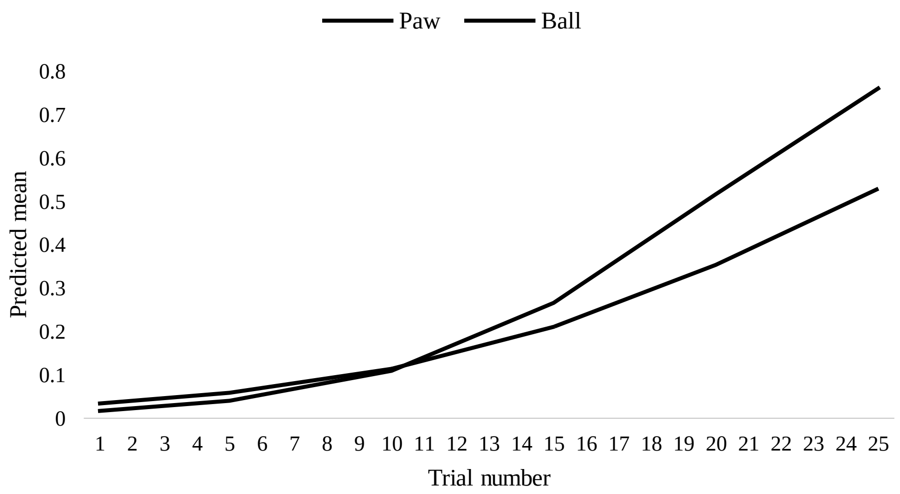

Figure 4. The logistic regression predicted probabilities of ball delivery (solid line) or paw use (dashed line) for the 16 cats. Changes over time were significant (p < 0.001). The trials on 16 cats lasted 3 minutes with a maximum of 3 per day and a total of 336 trials.

A logistic regression model was performed to analyse the association between cats and the two-way interaction with trial number, to investigate the individual cat performance (Figure 5). Overall, the cats followed individual learning curves, however the majority of the cats made the most progress between trials 10 and 20.

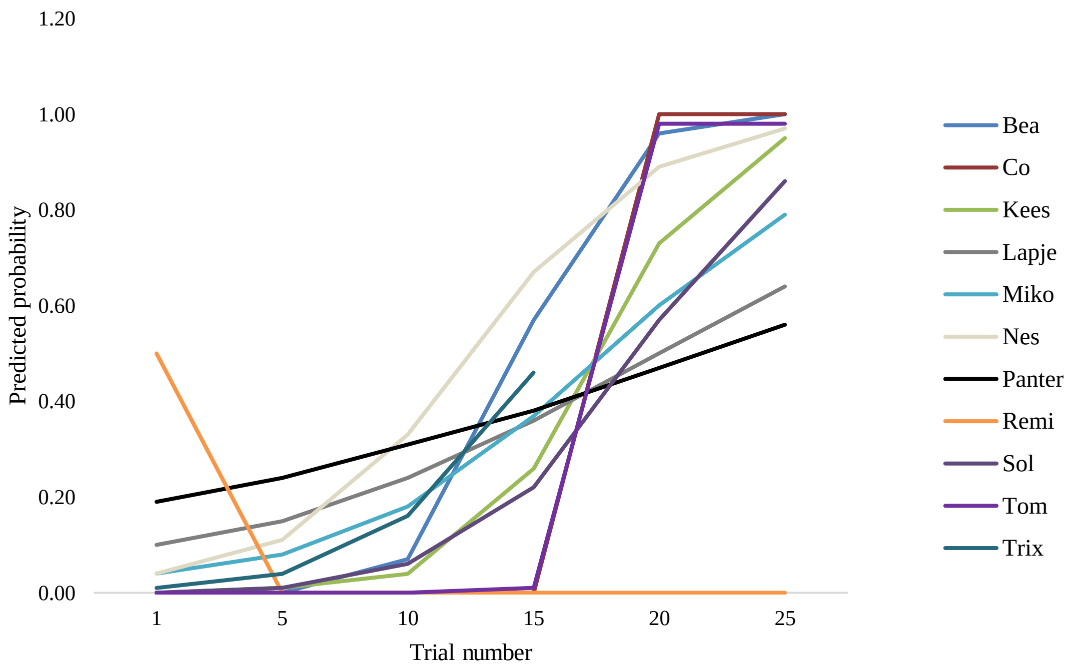

Figure 5. Predicted probability of nudging the ball into the receptacle for each individual cat, showing their use of the enrichment device by spontaneous trial and error learning. Only the cats that have put the ball in the receptacle at least once are included in this figure; 11 of the 16 cats.

Behavioural factors influencing ball deposit success

Video footage of trial numbers 1, 10, 15 and 25 for each cat was analysed using the ethogram (Table 1, Methods). This resulted in 53 trials on 16 different cats, due to some cats being eliminated after three consecutive mistrials, with a total of 159 minutes of video footage. The LMM predicted mean behaviour scores (Table 2) of these 53 records showed that the cats had mostly their ears in a neutral position. Their locomotive states differed between standing and either walking or sitting. They interacted with the device mostly via sniffing, but rubbing occurred also. Their tail position was mainly down, and at times in the upright position. They spent barely any time grooming. The predicted means of nudging the ball in (by paw and nose added up) and putting the paw in the receptacle occurred in similar numbers. They interacted with the food dispenser, mostly by sniffing the location of food dispenser (that was located just outside the metabolic cage). The fixed effects evaluated here are the successful delivery of the ball in the receptacle (yes, no), trial number (covariate 1 to 25) or two-way interactions between these two factors. Table 2 provides an overview of the (near) significant effects.

Table 2. Predicted means (μ) and the outcome of linear mixed model (LMM) for each behaviour that was observed, showing the significant effects and non-statistically significant trends. The LMM used the 53 records on 16 cats. Behaviours that were not observed are left out of this table.

Behaviour	μ ± s.e.	Ball delivery	Trial number	2-way interaction
Ears neutral[1]	96.7 ± 0.65		<0.001	0.031
Ears asymmetric[2]	1.63 ± 0.24			
Ears back[1]	2.84 ± 0.68		<0.001	0.074
Tail down[1]	78.47± 5.89			0.059
Tail upright[1]	20.86 ±5.77		0.055	
Interact with ball via play[1]	1.49 ±0.42	0.010	0.034	
Interact with device via sniff[1]	5.48 ±1.06	0.016	0.010	
Interact with device via rubbing[1]	1.3 ± 0.55		0.001	0.040
Interact with food dispenser[1]	10.0 ±3.05		<0.001	
Sit[1]	22.44 ± 3.92			
Stand[1]	55.69 ± 3.98	0.029		
Walk[1]	21.20 ± 2.62		<0.001	0.003
Eat[1]	1.90 ±0.49		0.004	
Groom [2]	0.13 ± 0.062			
Jump[2]	0.51 ±0.14		<0.001	0.008
Lick[2]	0.092 ± 0.053			
Meow[2]	4.13 ±0.92		<0.001	0.050
Nudge ball by paw[2]	0.097 ±0.018	<0.001	0.001	
Nudge ball by nose[2]	0.052 ± 0.015	<0.001	0.033	
Paw in hole[2]	0.12 ± 0.071			
Rub[2]	0.14 ± 0.057			
Tail quiver[2]	1.16 ± 0.25			

[1]) Expressed as percentage of the observation time. [2]) Expressed as rate per minute.
**Note: The significance of TrialNr was also scored but not discussed further since it was not relevant to this research.*

Interaction effects are the more precise representation of the main effects, so after having explained the former, the latter were ignored (Appendix III). Interaction effects occurred for the behaviours; ears in neutral position, ears in backward position, rubbing against the device, walking, grooming and meowing. Rubbing against the device was observed increasingly more when cats delivered the ball (Figure 6A). In the earlier trials, the ears in a neutral position were observed more when cats delivered the ball but this decreased over time (Figure 6B). Walking, jumping, and meowing were observed less when the ball was delivered, but at later trials were observed more compared to no ball delivery (Figure 6C, 6D and 6E), but these behaviours decreased over time.

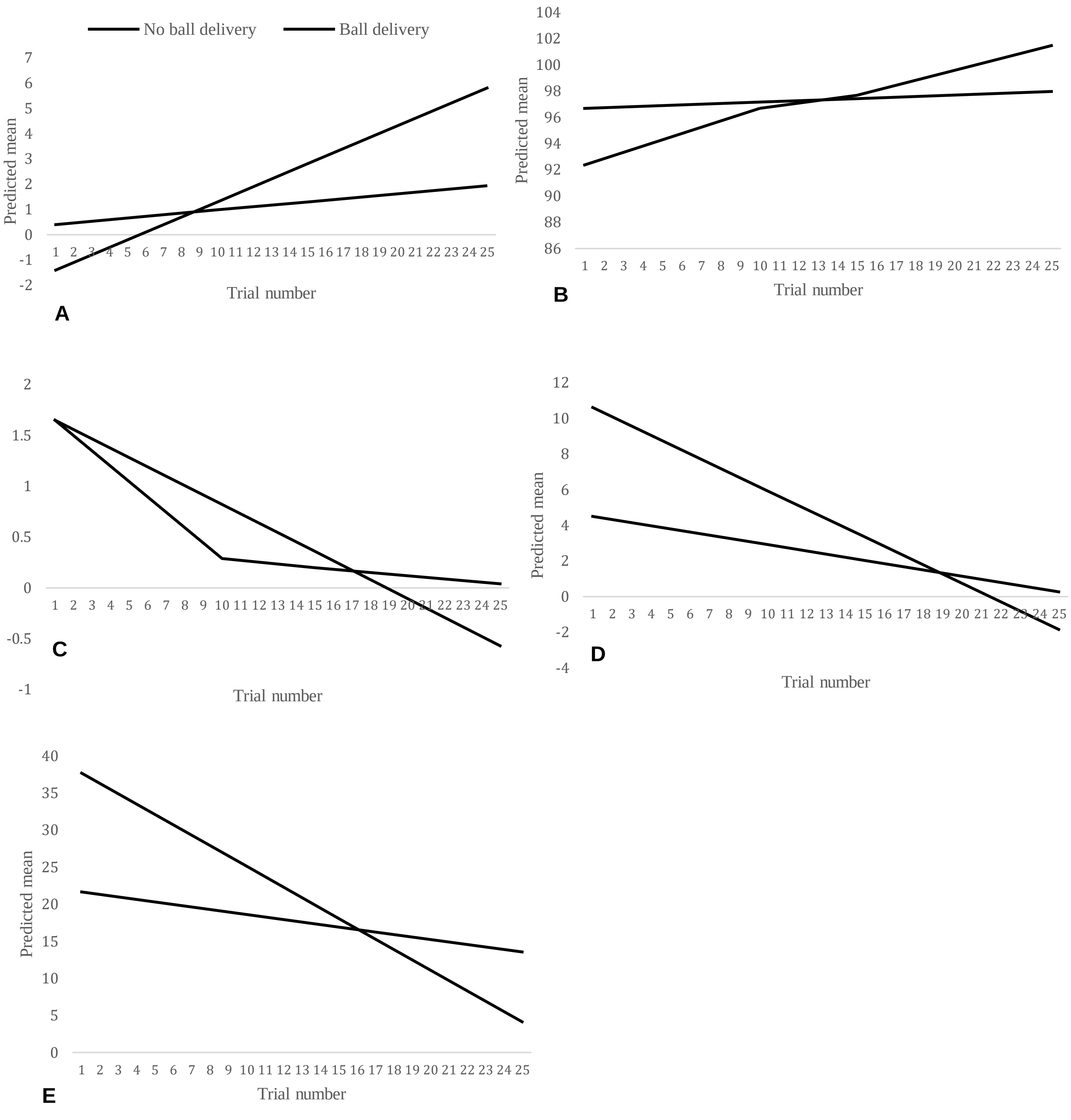

Figure 6. The five behaviours that had a significant effect of the two-way interaction between trial number and successful ball delivery after a linear mixed model (n=16) was performed. A) The interaction with device via rubbing (p=0.040). B) Ears in a neutral position (p=0.031) C) Jumping (p=0.008). D) Walking (p=0.003). E) Meowing (p=0.050).

Behaviours that occurred more when cats delivered the ball, regardless of trial number, were the interaction with the ball by playing (p=0.010), interaction with the device by sniffing (p=0.016), standing (p=0.029), nudging the ball by paw (p<0.001) and nudging the ball by nose (p<0.001) (see Table 3).

Table 3. Predicted means of the significant effect of ball delivery (successful or not) on the behaviours for the 16 cats.

	No ball delivery	Ball delivery
Interact with ball by playing	0.47	2.50
Interact with device by sniffing	3.44	7.52
Stand	48.83	62.54
Nudge ball by paw	0.00027	0.19
Nudge ball by nose	-0.0020	0.11

Using the same dataset of 53 trials (of 16 cats), a PCA was performed and found dimensions indicative of anxiety. Behaviours with loadings < ⎪0.4⎪ were omitted stepwise and the fifth analysis produced a 2-component outcome with 9 behaviours (Table 4). The first component seemed to reflect variation in anxiety and explained 43% of the variation. Cats that showed little signs of anxiety engaged in handling the enrichment device or food rewards, as opposed to the cats that showed more signs of anxiety. The first component grouped the behaviours walking (loading -0.84), meowing (-0.80), jumping (-0.77) and ears back (-0.77), inversely with ears neutral (0.80), eating (0.61) and paw in hole (0.45). High negative component scores identified cats that showed signs of anxiety, as opposed to the cats that had positive component scores (Appendix V). The second component explained 25% of the variation and identified cats who pawed the receptacle, whilst standing, and in this way retrieve food that they then ate. This second component grouped standing (-0.86), eating (-0.54) and paw in the hole (-0.60) inversely with sitting (0.87). Together with the first component, this means that cats who were not pawing the receptacle for food rewards were either anxious or sitting undisturbed.

Table 4. Loading scheme of the principal component analysis on 53 trials of 16 cats, producing a 2-component loading scheme, using a cut-off value of ≥│0.4│.

	Component 1 **43.3%**	Component 2 **24.9%**
Ears Neutral	0.80	0.14
Ears back	-0.77	-0.12
Sit	0.33	0.87
Stand	0.21	-0.86
Walk	-0.84	-0.21
Eat	0.61	-0.54
Jump	-0.77	-0.07
Meow	-0.80	-0.09
Paw in Hole	0.45	-0.60

With the outcomes of the PCA, an additional LMM test was performed to test for a relationship between the anxiety levels (PCA component 1) and the LMM effects of ball delivered in the receptacle, trial number and the two-way interaction (Appendix IV). The two-way interaction had a significant effect ($p = 0.002$) and this is shown in Figure 7. Negative component scores indicated anxiety (component 1 of PCA), and especially in the earlier trials it is visible that the cats that were unsuccessful in delivering the ball were more anxious. Likely, the cats that were stressed and thus anxious during the initial trials were then unable to understand how the enrichment device operated. Overall, cats got less anxious during the duration of the study.

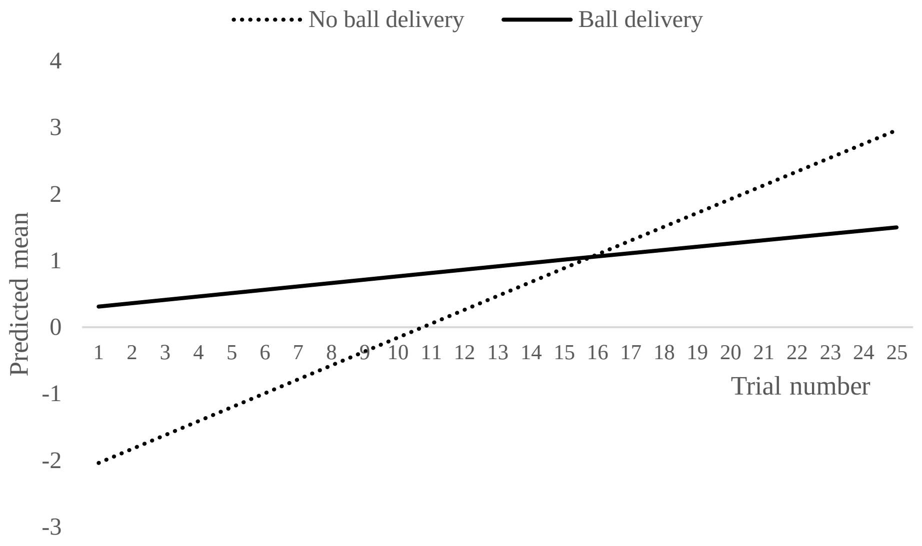

Figure 7. The significant two-way interaction effect of trial number and ball delivery on the first component of the principal component analysis (p=0.002). This first component represents anxiety and is based on the 53 trials of 16 cats.

Spearman's Rank correlations were calculated between the predicted success (i.e. ball delivery) and the outcome of previous personality tests on the 16 cats. The predicted success was expressed as the average PCA component score per cat or the predicted probability of delivering the ball. Previous tests on personality included an open field test, novel object test, delay discount test (max delay as index of choice impulsivity) and reversal learning test (max days needed to relearn). A significant positive correlation existed between the predicted probability of ball delivery and reversal learning ($n = 16$, $r = 0.61$, $p = 0.012$). The direction of the relationship is unexpected, and possibly cats that readily learn a new operant or association have more difficulty in then unlearning it.

The chance on successful ball delivery was unrelated to the sex of the cats ($\chi^2 = 2.13$ with a critical value of 3.84, df = 1).

Discussion

Feline welfare in captivity can be improved by using environmental enrichment to stimulate natural hunting behaviours. For feasibility reasons, cats should be able to operate the enrichment device without training, but it is unclear if cats can manage this by spontaneous trial-error-learning. In this study, we investigated whether colony-living domestic cats could learn to operate a reversed vending device via trial-and-error, by nudging a ball in the receptacle in return for a food reward, and which factors might influence this learning process. Cats could nudge a ball in a receptacle during 3-minute trials in a metabolic cage and video recordings of the cats' behaviours were analysed for 53 of the 336 trials. The predicted probability of a cat rolling the ball into the receptacle was 0.15 and the likelihood increased significantly with the trials. There was a clear learning curve, indicating that the cats learned the required operant via spontaneous trial-and-error. Eleven of the 16 cats managed to put the ball in the receptacle, and ten of those showed a learning curve with the most progress made between trials 10 and 20. Surprisingly, the best-performing cats struggled with reversal learning in earlier tests. Factors that influenced the learning process were classified as anxiety, and this negatively influenced the cats' learning ability. The cats learned spontaneously to nudge a ball in a hole for a food reward, but the full use of the present enrichment device would require more shaping steps and learning time.

Our colony-living domestic cats learned by trial-and-error to nudge a ball into a receptacle for a food reward. The same was true for some cats that put their paw in the receptacle, thus receiving a food reward by an alternative strategy. Cats using their paw, instead of the ball, was not a behaviour that the device ultimately will be used for, but it is still an effective operant learned by trial-and-error. The cats significantly increased these operants, both nudging the ball and their paw in the receptacle, over time and showed a learning curve via trial-and-error. Our results agree with a study done on 30 cats, where one group (n = 15) had a human demonstrate an operant to solve a transparent tube and drawer task and a control group (n = 15) without a human demonstration (Arahori et al., 2023). Both groups showed a similar success rate, indicating that the cats used a trial-and-error process to learn rather than learning from the human demonstration. However, not all studies agree with cats' ability for trial-and-error learning, as when cats (n = 53) were tested on a classic detour task with a transparent V-shaped fence (Pyari et al., 2022). If successful, the cats showed no significant change in their latency to reach the food during the trials. It also showed that cats chose a side (of the V-shaped fence) irrespective of their first trials' success, concluding that the cats did not use effective trial-and-error learning. However, this study only had three trials, while our study showed the most progress in learning to be between trials 10 and 20. So performing only three trials might have given the cats insufficient time for repeated trial-and-error.

Behaviours associated with an increased learning ability may help to identify ways to promote the (speedy) use of an enrichment device. Walking, jumping and meowing all had an inverse relationship with success rate and learning. These behaviours occurred more when cats were unsuccessful in delivering the ball. These three behaviours, together with ears in a backward position, were associated together in this study and reflect an anxious mood. The "2015 AAHA Canine and Feline Behavior Management Guidelines" indicate signs of anxiety in domestic cats to be pacing (increased activity), vocalization and the lowering of ears (Hammerle et al., 2015). The Cat Stress Score by Kessler and Turner (1997), a commonly used tool to measure stress in cats, also considers ears back, increased activity and increased vocalization to be associated with anxiety in cats. Regarding vocalizations, the cats ($n = 8$) were exposed to a 3-minute spray bath, which induced meowing in correlation with increases in plasma cortisol levels ($r = 0.93$, $p < 0.001$), indicating that meowing is associated with stress and anxiety (Iki et al., 2011). Regarding ear position, cats ($n = 47$) were held in a full-body restraint for two minutes, which is known to cause stress in cats. They showed significantly more often their ears in a backward position compared to a passive, less stressful, restraint (Moody et al., 2018). Increased activity, by walking and jumping, can be seen as pacing and a sign of frustration or anxiety (Kessler & Turner, 1997), but the meaning of hyperactivity is difficult to assess. Fear can render cats motionless and behaviourally inhibited or frantically trying to escape (Shu & Gu, 2021). However, since there was no reason for fear in this study, we assume the cats were either relaxed or somewhat anxious, but not fearful. Overall, this study showed that behaviours associated with anxiety were negatively related to learning in cats.

Anxiety can impair learning performances, as demonstrated in rats. Rats ($n = 40$) were divided into two groups, where one group was exposed to two methods to induce anxiety (elevated T-maze and cat odour exposure increased anxiety was confirmed by their corticosterone levels) while the other group acted as non-stressed controls (Küçük et al., 2008). Their search times during a Moris water maze test were recorded to test for their spatial learning abilities and the anxious rats took a significantly longer time to find the platform, indicating anxiety impaired their learning ability. During our study, the observed anxiety decreased over time. It could be the anxiety observed in our study was caused by the novelty aspect of the test, and that the cats got more relaxed over time in the test setting. Another explanation is that the cats that showed unruly behaviour may have been the more anxious cats and their removal may have caused the observed reduction in anxiety over time.

In addition to anxiety, there were a couple of other behaviours connected to a successful ball deposit. However, most are easy to explain since they require interaction with the device or ball thus increasing the chances of the ball going in the receptacle. Nudging the ball, both by paw and nose, and playing with the ball were directly associated with the success rate. Because the receptacle device had a slight slope, any (accidental) physical interaction with the ball would often cause it to go into the hole. Cats that played with the ball had a higher success rate, since it required touching the ball. Playing behaviour is also seen as a sign that the animal is in good welfare, or at least the absence of negative emotions such as stress (Delgado & Hecht, 2019). This would make the chances of trial-and-error learning higher when playing behaviour is involved. Cats could be stimulated to play with the ball by using balls in play sessions beforehand, as this may be tested as a strategy to speed up trial-and-error learning. Play behaviour could be encouraged by giving them the ball before dinner time. A group of cats ($n = 9$) were tested on the effects of different hunger states on their play behaviour (Hall & Bradshaw, 1998). When hungry, cats were significantly more likely to play with a small toy, including kill-bite and clutching, than when the cats were not hungry ($p < 0.01$).

The cats from this study were all the same age (appr. 1 year of age), and there learning abilities might still be in development. However, when cats ($n = 36$) of different ages were tested on food finding and motor function tests, there was no significant effect of the cats' ages on their ability and time to learn a new task (McCune et al., 2008). The food finding test was done via a holeboard-box and the motor function test was done via plank-walking test. This study compared young, adult, senior and even geriatric cats. Therefore, the results from our study likely apply to cats of all ages.

During the study, the cats were able to see and interact with the food dispenser. While the food itself was in a closed container and out of reach, it was visible and some cats were able to figure out that when they rattled the railing of the cage (using their paws) kibble would fall out. For future applications, it would be better to have the food not visible nor reachable for the cats, so they will focus on the task at hand, which is the ball receptacle. For the enrichment device, different setups were tried, such as a bigger platform for the ball and adding an extra ball to increase the chances of them succeeding via trial-and-error. These observations were excluded in this study, but can be promising for further research. This study is part of a larger effort to improve the welfare of (big) cat species in captivity. The domestic cats in this study showed that they can learn an operant behaviour via spontaneous trial-and-error. This gives great promise to the applicability of this device for bigger cat species without any human interference. Big cat species and domestic cats are from the same family (*Felidae*) and their morphology is relatively similar (Kitchener et al., 2010). In addition to this, the behavioural repertoire of big cat species and domesticated cats are similar (Cameron-Beaumont, 1997). This has great promise for the big cat species in captivity to be able to learn how to use this enrichment device by trial-and-error.

Overall, the domestic cats in this study learned a required operant behaviour via trial-and-error. Play was associated with successful learning, contrary to stress-related behaviour and anxiety seems to impair the learning ability of the cats. This study this is a promising first step and warrants further research, with more shaping steps for the cats to fully use the enrichment device, ultimately leading to the implementation of an enrichment device that stimulates hunting behaviour in (big) cat species in captivity as to improves their welfare.

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Appendices

Appendix I. Cats (n=16) with the corresponding number of trials in which they successfully deposited the ball into the receptacle. If a cat was prematurely removed, it will state after which trial and the reason for removal. If not removed, each cat had a total of 25 trials.

Cat name	Number of trials with successful ball deposit	Removed	Why removed
Bea ♀	12		
Eva ♀	0	Yes, after trial 15	Unruly behaviour by feeding station
Fea ♀	0	Yes, after trial 12	3 consecutive trials with paw in receptacle
Lapje ♀	4	Yes, after trial 16	3 consecutive trials with paw in receptacle
Luna ♀	0	Yes, after trial 16	Unruly behaviour by feeding station
Panter ♀	9		
Sol ♀	6	Yes, after trial 24	Unruly behaviour (continuous meowing)
Trix ♀	11		
Co ♂	6		
Jerry ♂	0		
Kees ♂	8		
Log ♂	0		
Miko ♂	7	Yes, after trial 23	3 consecutive trials with paw in receptacle
Nes ♂	12		
Remi ♂	1		
Tom ♂	1		

Appendix II. Predicted mean (± s.e.) per individual cat (n = 16) of their successful ball deposit and the cats putting their paw in the receptacle. Outcome of logistic regression model. Note that this is an underestimation for the paw in receptacle, since cats that put their paw in the receptacle three trials in a row, were eliminated from the study.

Cat name	Prediction of successful ball deposit	s.e.	Prediction paw in receptacle	s.e.
Bea ♀	0.16	0.14	0	0
Co ♂	0.00	0.00	0.02	0.04
Eva ♀	0.00	0.00	0	0
Fea ♀	0.00	0.00	0.98	0.05
Jerry ♂	0.00	0.00	1	0
Kees ♂	0.08	0.08	0.62	0.16
Lapje ♀	0.28	0.12	0.51	0.18
Log ♂	0.00	0.00	0	0
Luna ♀	0.00	0.00	0	0
Miko ♂	0.24	0.11	0.02	0.06
Nes ♂	0.44	0.14	0	0
Panter ♀	0.33	0.10	0.15	0.11
Remi ♂	0.00	0.00	0	0
Sol ♀	0.09	0.08	0	0
Tom ♂	0.00	0.00	0	0.01
Trix ♀	0.24	0.12	0.09	0.06

Appendix III. The predicted means (± s.e.) of the cats' (n=16) behaviours with a significant effect (and trend) of the two-way interaction of trial number and successful ball deposit. This is the outcome of the linear mixed model of 159 minutes of 53 trials in total. The significant effects are also visualised in a graph in Figure 6.

Ears neutral (p=0.031)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	92.38 ±0.96	96.69 ±0.66	97.69 ±0.83	101.48 ±1.52
Ball Score 1	96.69 ± 1.97	97.17 ± 1.15	97.44 ±0.99	97.98 ±1.60

Interact with device by rubbing (p=0.040)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	0.40 ±0.76	0.98 ±0.56	1.30 ±0.68	1.94 ±1.18
Ball Score 1	-1.40 ±1.52	1.30 ±0.92	2.80 ±0.80	5.81 ±1.25

Walk (p=0.003)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	37.67 ±3.06	25.09 ±2.68	18.11 ±2.93	4.14 ±4.11
Ball Score 1	21.65 ±5.28	18.62 ±3.54	16.93 ±3.22	13.56 ±4.44

Jump (p=0.008)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	1.65 ±0.19	0.82 ±0.38	0.36 ±0.17	-0.57 ±0.29
Ball Score 1	1.65 ±0.38	0.29 ±0.23	0.20 ±0.20	0.04 ±0.31

Meow (p=0.050)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	10.61 ±1.21	5.94 ±0.94	3.35 ±1.11	-1.84 ±1.82
Ball Score 1	4.50 ±2.36	2.92 ±1.46	2.04 ±1.28	0.27 ±1.95

Ears back (p=0.074)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	6.48 ±0.97	3.72 ±0.70	2.18 ±0.86	-0.89 ±1.52
Ball Score 1	2.62 ±1.97	2.27 ±1.17	2.07 ±1.02	1.68 ±1.61

Tail down (p=0.059)

	Trial 1	Trial 10	Trial 15	Trial 25
Ball Score 0	67.20 ±7.00	75.56 ±6.02	80.21 ±6.64	89.51 ±9.59
Ball Score 1	87.45 ±12.37	81.18 ±8.16	77.69 ±7.38	70.72 ±10.37

Appendix IV. Outcome of the linear mixed model of component 1 (reflecting anxiety) of the principal component analysis (n=16). The two-way interaction of the trial number and successful ball deposition had a significant effect.

Behaviour	**Predicted mean (±se)**	**Ball score**	**Trial number**	**two-way interaction**
PCA component 1	0.41 ±0.29	0.332	<0.001	0.002

Appendix V. Outcome of the principal component analysis on each trial. If not prematurely excluded, each cat (n=16) had a total of 25 trials. Trial 1, 10, 15 and 25 were observed and analysed, resulting in a total of 53 trials. Negative scores in the first component indicate an anxious mood during that trial.

Cat_TrialNumber	Component 1	Component 2
Bea_1	-0.932	-0.128
Bea_10	-0.318	0.474
Bea_15	0.347	0.441
Bea_25	1.164	-0.097
Co_1	-4.551	-0.785
Co_10	-2.133	-0.639
Co_15	-0.172	1.968
Co_25	0.516	-0.448
Eva_1	-0.43	-0.314
Eva_10	1.334	0.979
Eva_15	1.464	-1.39
Fea_1	-1.355	-0.407
Fea_10	4.205	-4.892
Jerry_1	0.608	-0.337
Kees_1	-2.496	-0.887
Kees_10	2.126	-1.971
Kees_15	1.823	-0.627
Kees_25	1.638	0.994
Lapje_1	-1.431	-0.682
Lapje_10	1.23	-1.55
Lapje_15	3.036	-3.345
Log_1	-4.447	-0.114
Log_1	-0.653	1.279
Log_15	0.836	0.394
Log_25	-1.608	0.454
Luna_1	-2.506	0.07
Luna_10	0.457	0.873
Luna_15	1.199	-1.409
Miko_1	-1.008	-1.115
Miko_10	0.884	1.319
Miko_15	0.101	-0.204
Nes_1	-4.351	-0.176
Nes_10	1.451	-0.875
Nes_15	1.562	0.774
Nes_25	0.477	0.82
Panter_1	-3.351	-0.301
Panter_10	1.013	1.931
Panter_15	1.239	-0.42
Panter_25	2.005	1.06
Remi_1	-1.017	-0.482

Remi_10	1.234	3.011
Remi_15	1.864	3.591
Remi_25	1.645	3.215
Sol_1	-3.483	-1.358
Sol_10	1.155	-0.572
Sol_15	0.042	0.053
Tom_1	-2.026	0.132
Tom_10	0.755	2.503
Tom_15	0.223	2.165
Trix_1	-3.054	-0.67
Trix_10	0.692	-0.981
Trix_15	-0.08	-1.154
Trix_25	3.078	-0.174

Appendix VI. Synthetic time budget (outcome from BORIS), showing the duration and occurrence of all behaviours, tallied using the ethogram. Total of 53 trials on 16 cats, which resulted in 159 minutes of footage analysed. Maximum of four trials per cat; trial 1, 10, 15 and 25.

	Behaviors:	Ears invisible	Ears neutral	Ears asymmetrical	Ears back	Ears flat	Eating	Grooming	Interact with ball	Interact with ball	Interact with device	Interact with device	Interact with feed dispenser	Jumping	Laying	Laying	Laying	Licking	Meowing	Nudge ball	Nudge ball	Out of sight	Paw through opening	Rubbing	Sitting	Standing	Tail down	Tail invisible	Tail quiver	Tail upright	Walking
	Modifiers:								Play with ball	Bite ball	Sniffing device	Rubbing device			Head down	Head up	None			Paw	Nose										
Bea1	191,32	67,668304	92,865803	0	6,464911	0	0	0	0	0	5,74325737	0	1,895365442	0,6272214	0	0	0	0	3,136107	0	0	3,3702697	0	0	14,604699	53,084837	76,520652	18,503032	3,8481272	23,441508	32,171448
Bea10	181,97	16,795076	92,969988	1,188840748	6,9243369	0	0	0	6,99798316	0	0,41710172	0	14,8540049	0,3297247	0	0	0	0	0,3297247	0,3297247	0	2,8295873	0	0,6786524	28,276053	48,581899	70,98028	36,518107	2,0775983	28,842258	23,0821
Bea15	209,99	27,088433	95,682105	1,175648403	4,0729686	0	1,1429116	0	0	0	0	0	0,727457775	0,2857279	0	0	0	0	0	0,2857279	0,2857279	1,7405591	0	2,0355248	28,373276	48,696537	41,086002	40,890042	0	51,559315	22,884145
Bea25	190,86	12,009326	97,193028	1,071817743	2,6735898	0	3,4580321	0	0,93426992	0	9,16902442	0	5,897278385	0	0	0	0	0	0	0,3143666	0	1,9150162	0	0	24,706071	58,081248	60,906887	11,617416	1,067065	9,0119571	17,086082
Co1	195,07	80,159943	83,905225	0	15,464317	0	0	0	0	0	0	0	0	1,8454914	0	0	0	0,309975	16,609422	0	0	0,7720306	0	0,929925	3,0987167	41,848691	64,289211	32,97688	0,9178382	35,574643	49,33872
Co10	192,01	38,996927	92,633098	5,122425981	7,2806748	0	0	0	0	0	0,7801677	0	0	0	0	0	0	0	13,124316	0	0	1,3832613	0	0	0	48,569346	76,932587	18,278215	1,5295002	22,947602	51,332425
Co15	191,32	3,2181685	98,487819	1,944232919	1,3496217	0	0	0	0	0	0	0	0	0,6272214	0	0	0	0	9,0947104	0	0	2,0405603	0	0	51,493469	20,007363	90,606959	10,2765	0,6990603	9,3580878	28,325757
Co25	192,51	17,619864	97,410934	0,756668138	2,5260105	0	2,1817048	0	7,55755384	0	31,1776012	8,834865721	2,637047351	0	0	0	0	0,3164457	0,3116721	0	0,3116721	1,5084931	0	0	10,154742	58,392667	85,917987	83,278791	0	13,957751	31,303334
Eva1	188,97	74,36736	99,634584	2,477393782	0	0	0	0,961482	0	0	1,98073768	0,660422289	0	1,2700429	0	0	0	0	11,430386	0	0	0,9308356	0	0	9,373915	61,157731	77,562245	30,243954	0	22,384652	27,886716
Eva10	186,8	6,7708779	98,957807	1,033579861	0,8527034	0	0	0	0	0	0	0	38,0366245	0	0	0	0	0	2,248394	0	0	0,7521413	0	0	39,147226	53,801882	98,601929	17,483405	0	1,2994596	7,0098978
Eva15	51,17	7,6392417	98,821438	0	0,5289774	0	3,5176861	0	0	0	0	0	69,19617879	0	0	0	0	1,2433429	0	0	0	5,6927887	0	0	0	82,914396	93,657628	36,001563	0	6,076707	16,950909
Fea1	191,02	67,915402	87,71864	3,915937867	2,0216029	0	0	0	0	0	3,2624856	0	0,805046818	1,2564129	0	0	0	0	9,7372003	0	0	2,3280285	0	0	13,729211	61,117096	98,30411	19,863889	0	1,6357888	22,346749
Fea10	83,03	9,024449	99,718019	1,588625442	0	0	12,284716	0	0	0	4,21413947	2,407563531	0	0	0	0	0	0	0	0	0	1,9884379	2,167891124	0	0	94,026715	99,506751	61,908949	1,8971132	0	5,5272245
Jerry1	193,54	71,743826	99,645254	3,291458665	0	0	1,5500672	0	0	0	2,44755606	0	4,078529183	0,6200269	0	0	0	0	2,4801075	0	0	1,8063449	0	0	9,3404685	59,467281	99,88306	27,979746	0,8609062	0	26,970596
Kees1	200,75	77,894396	88,489533	0	11,294139	0	0	0	0	0	0	0	0,79580106	0,8966376	0	0	0	0	9,5641345	0	0	53,116314	0	0	10,883031	64,440761	94,64204	59,734496	1,4845422	4,9682679	40,607104
Kees10	191,89	12,187712	99,839765	0,356076746	0	0	5,0028662	0	0	0	10,0234509	0	26,94162328	0	0	0	0	1,600239	0	0	0	2,3023607	0,312679139	0	0	88,184902	99,714515	49,435614	0	0	11,753222
Kees15	197,72	11,956808	99,844324	1,034013293	0	0	3,3380538	0	0	0	12,774125	13,61167307	2,953406492	0	0	0	0	0	0	0	0	1,6007485	0,606918875	0	22,610573	55,880856	96,362112	8,2975926	0,6618353	3,453677	21,45049
Kees25	191,04	22,978957	99,848445	0,407772137	0	0	2,8266332	1,6139098	0,39654025	0	16,6195561	11,12123116	0	0	0	0	0	0	0	0,6281407	0	2,6989112	0	0	41,686751	42,210196	86,140238	71,594954	0	13,808164	16,002453
Lapje1	195,8	71,603677	99,52518	3,237410072	0	0	0	0	0	0	4,59959142	3,705822268	9,739629203	2,7579162	0	0	0	0	12,563841	0	0	9,5342186	0	0	0	59,963756	5,9016149	17,648621	0,7442137	93,935898	36,530384
Lapje10	189,01	13,833131	99,489144	1,473622163	0,3082326	0	5,0790963	0	0	0	10,7142479	4,493413047	11,28926526	0,3174435	0	0	0	0	3,4918787	0,3174435	0	1,5364266	0	0,6447938	0	79,384867	74,009298	25,341516	2,9763592	25,866687	20,554415
Lapje15	106,33	10,970563	99,939788	0,633813976	0	0	8,4642152	0	0	0	0	1,195335277	12,04839878	0	0	0	0	1,206952	0	0	0	6,4948744	1,692843036	0	0	70,276794	44,669262	55,797047	2,5531372	55,326482	18,112327
Log1	190,72	76,485424	94,496845	4,013646398	2,2320334	2,7872544	0	0	0	0	0	0	0	5,033557	0	0	0	0	19,190436	0	0	11,056523	0	0	6,1857068	25,487376	95,978256	24,474622	1,2496355	3,819025	66,930963
Log10	204,37	26,71625	98,117113	3,605528477	1,66522	0	0	0	0	0	0,48979792	0	4,76611211	0,5871703	0	0	0	0	9,1011401	0	0	2,5307041	0	0	35,006878	24,965612	97,227703	21,634291	1,1239042	2,6561602	40,003916
Log15	194,09	17,218301	99,905397	1,493735646	0	0	0	0	8,73394806	0	1,54722036	0	24,84751609	0	0	0	0	0	2,7822144	0	0,3091349	2,0124684	0	0	21,813612	54,10392	100,53537	35,040445	2,3794416	0	24,006751
Log25	186,69	15,779635	95,523783	3,816041366	4,4520483	0	0	0	0	0	1,2030639	0	0	0,9641652	0	0	0	0	15,426643	0	0	0	0	0	24,403021	38,760512	95,144809	24,041459	1,6924411	4,772684	36,783438
Luna1	195,41	77,958139	91,100947	1,393016345	8,7342125	0	0	0	0	0	4,48492912	0	0	1,8422803	0	0	0	0	13,203009	0	0	19,436569	0	0	24,766085	46,20305	58,041825	32,559234	1,8211343	41,745709	35,672589
Luna10	187,87	17,509448	99,1618	0,774318438	0,8117438	0	0	0,3217745	0	0	0	0	9,836645823	0,3193698	0	0	0	0	9,5810933	0	0	0,7473253	0	0,643549	35,727157	49,109221	89,518114	32,973865	3,8118835	10,154699	15,016679
Luna15	64,25	20,171206	97,426399	0	2,4351725	0	1,8677043	0	0	0	0	0	65,92877282	0	0	0	0	0	0,9338521	0	0	7,2622568	0	0	0	90,771012	49,054078	65,11751	2,6771372	50,191862	9,2038131
Miko1	200,28	77,3572	92,251207	2,646144347	6,0376194	0	2,0970641	0	0	0	1,87038147	0	1,259346276	0,5991612	0	0	0	0	10,784901	0	0,2995806	10,317056	0	0	5,8379775	69,470596	50,661586	32,90693	0	49,129296	25,866705
Miko10	190,26	12,580679	98,134965	2,885933479	1,8061134	0	0,6307159	0	0	0	2,88867865	0	0	0	0,8093288	9,553201	0	0	0,3153579	0	0	2,3268159	0	0	36,806165	32,943557	67,989025	37,358877	0,503436	31,859105	19,276447
Miko15	198,78	12,805111	95,300763	1,384673967	4,6271188	0	1,5092062	0	11,185832	0	32,1601771	1,515242982	0	0,6036825	0	0	0	0	0,9055237	0	0,3018412	1,9649864	0	0	18,234346	58,904215	6,7197399	51,405574	1,8634312	92,952089	22,827057
Nes1	192,13	68,774267	83,253325	4,00040004	16,276628	0	0	0	0	0	1,17108208	0	1,776653914	3,1228855	0	0	0	0	5,9334825	0	0	4,9065737	0	0	17,60617	34,909115	66,353508	26,094832	0,8451061	33,455639	47,39331
Nes10	199,82	19,626164	98,637012	0,74718405	1,2465521	0	4,2037834	0	5,00280998	0	7,50675608	1,627464718	0	0	0	0	0	0,3086197	0	0,3002702	0	2,7054349	0	0	11,016696	71,121936	95,754252	68,516665	0	3,5638213	17,742035
Nes15	200,65	6,9379517	99,862903	1,927927638	0	0	0	0	0	0	3,03463743	0	1,664946716	0	0	0	0	0	0	0,2990282	0	2,4460503	0	0	33,646841	57,263132	94,693551	53,951159	0	5,115967	8,9362528
Nes25	186,4	9,0069742	96,019126	3,537506412	3,8157902	0	0,9656652	0	0	0	2,13733906	1,884120172	0	0	0	0	0	0	2,5751073	0,3218884	0	1,4286481	0	0	36,326924	44,779767	71,639436	11,934549	0	0	18,842149
Panter1	194,22	84,229739	83,398087	1,958927814	16,069738	0	0	0	0	0	5,03192256	0	0	0,617856	0	0	0	0	7,7232005	0	0	4,4645248	0	0	14,143973	40,745032	94,237565	16,072495	1,1042674	5,6630512	44,261624
Panter10	186,94	6,1137263	99,900291	1,025576744	0	0	0	0	0	0	9,90371242	0	0	0	0	0	0	0	3,8515032	0	0	1,0195785	0	0,3242647	51,451085	29,038987	94,255913	16,250669	1,916186	5,4394134	18,256104
Panter15	197,85	24,035886	97,991284	1,197644632	1,9781097	0	2,4260804	0,6171982	8,596844	1,155703683	13,4546374	3,407632044	2,845283834	0	0	0	0	0	0	0	0	1,7300986	0,303260045	0	20,367027	59,17028	90,405213	44,930503	1,6520582	9,1606627	20,406116
Panter25	182,57	15,824615	97,844208	0,780848392	2,1128456	0	4,600975	0,3286411	4,05253786	0	4,79268226	11,91159555	0	0	0	0	0	0	0,6572821	0	0,3286411	0	0,328641069	0	58,3798	35,959906	99,688417	27,046612	0	0	5,6142849
Remi1	198,49	85,596252	99,41588	0	0	0	0	0	0	0	2,64446572	0	0	1,8136934	0	0	0,9573894	0	7,2547735	0	0	7,6472366	0	0	0	53,288128	15,229628	28,93647	0	84,55556	45,619194
Remi10	196,27	54,140725	99,686695	1,333214825	0	0	0	1,5697437	0	0	2,41758802	0	0	0,917104	0	0	0	0	0	0	0	2,6269934	0	0	74,952646	15,165294	86,599669	61,468895	0	13,219174	9,6821792
Remi15	202,25	17,75377	99,9483	1,442801921	0	0	0	0	0	0	2,3461063	0	0	0,2966625	0	0	0	0,3059757	0	0	0	3,0437577	0	0	88,478485	11,474599	84,724388	85,41508	0	15,258662	0
Remi25	186,12	59,981195	99,936898	0,805552945	0	0	0	0	0	0	1,344294	0	0	0,3223727	0	0	0	0,3274877	0,3223727	0	0	1,5618956	0	0	79,878065	15,019677	53,838286	90,019342	0	44,439061	4,912861
Sol1	186,88	85,244542	86,201269	2,175883953	13,592022	0	0	0	0	0	2,00984589	0	0	1,9263699	0	0	0	0	19,58476	0	0	2,0997432	0	0	4,0977066	72,329413	87,906597	30,611087	3,7015901	12,050218	23,53462
Sol10	181,816	21,121353	97,607625	1,673476787	2,0925433	0	2,9700356	1,0833323	0	0	10,3082237	0	10,8309159	0,330004	0	0	0	0	2,6400317	0,330004	0	8,6142034	0	0	18,157252	72,527896	86,841582	30,885621	0,9549502	13,148869	9,1836489
Sol15	204,65	30,36257	97,401641	2,105071116	2,4453909	0	0	0	0	0,503460661	14,5360371	0	6,68321327	1,1727339	0	0	0	0	4,1045688	0	0	3,1380406	0	0	20,545533	61,041326	77,962518	24,881994	1,5611888	21,950315	18,264322
Tom1	199,89	70,541298	94,653987	2,037870425	5,0776938	0	0,3001651	0	0	0	1,62289259	0	0	1,2006604	0	0	0	0	21,912052	0	0	7,7282505	0	0	23,206211	45,891934	66,585827	32,5454	2,6699299	33,256202	30,733239
Tom10	191,19	25,964224	97,520293	0,847762965	2,2953182	0	0	0,6433764	0	0	0	0	2,01484055	0	0	0	0	0	3,4520634	0	0	2,4446885	0	0	65,132214	19,438011	99,003244	15,516502	6,314851	0,9286546	15,410474
Tom15	197,83	13,099631	93,373469	0,69801937	6,5445133	0	0	0,3090028	0	0	5,55881312	0	0,517064679	0,6065814	0	0	0	0	0	0	0	1,8485568	0	0	61,110968	24,723314	99,888871	30,405904	0	0	7,7291899
Trix1	191,06	80,976133	91,363799	0	8,231766	0	0	0	0	0	1,04626819	0	1,096816171	2,5122998	0	0	0	0	11,619387	0	0	4,2745734	0	0	3,689589	49,473189	19,944671	22,619073	1,2174995	80,007981	46,660616
Trix10	183,28	11,553361	98,597822	1,480521884	1,2313007	0	1,9642078	0	0	0	10,9062636	0,410846792	66,92528168	0,6547359	0	0	0	0	2,9463117	0,327368	0	0,6307289	0,327367962	0	8,5183721	66,5876	66,431143	43,320602	1,1551568	33,421574	24,835277
Trix15	189,97	29,567826	96,764574	2,242152466	3,1748879	0	0	0,3242157	6,21670003	0	4,86603148	11,0591146	13,1010148	0,6316787	0	0	0	0	0,3158393	0	0	2,5835658	0,631678686	0	1,3508986	57,252704	1,9310239	45,098173	2,876401	97,930909	41,329392
Trix25	193,23	3,1982611	97,719861	0,320769848	2,1395349	0	13,041453	0	0	0	2,72110956	0	3,314530865	0	0	0	0	0	0	0	0	2,2900171	0,31051079	0	56,45931	41,9348	90,231189	5,7811934	0	9,4694577	1,5910596