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# Ferrets' (*Mustela putorius furo*) enrichment priorities and preferences as determined in a seven-chamber consumer demand study

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ABSTRACT

Knowledge of species-specific motivation and preferences for enrichment options is necessary to put in place an appropriate enrichment plan. This knowledge is currently lacking for ferrets. Therefore, seven female ferrets were consecutively housed in a seven-chamber closed economy consumer demand set-up consisting of a corridor that was connected to six enrichment chambers (EC) and an empty control chamber (CC) via weighted doors. In each EC, enrichments from the categories tunnels, balls, water bowls, foraging, sleeping and social enrichment were placed in random order. Motivation to reach EC was measured by daily increasing the doors' weight until the ferret no longer entered EC (the maximum price paid, MPP). Preferences within a category were evaluated by comparing interaction times with the enrichments. Ferrets pushed the highest weights for sleeping enrichment (MPP 1450 ± 120 g). MPPs for water bowls (1075 ± 153 g), social enrichment (995 ± 267 g), foraging enrichment (950 ± 228 g) and tunnels (940 ± 393 g) were also significantly higher than for CC. Compared to other enrichments, inter-individual variation in motivation for access to tunnels was very high. Ferrets preferred the hammock (9.2 ± 5.9 h) over the Savic Cocoon® (0.6 ± 0.8 h; $P = 0.011$) within the category sleeping enrichment; the large (5.8 ± 1.7 min) over the small water bowl (3.1 ± 0.8 min; $P = 0.014$) within the category water bowls; the flexible (6.1 ± 2.6 min) over the rigid tunnel (0.3 ± 0.2; $P < 0.001$) within the category tunnels; and the ferret ball (0.9 ± 0.5 min) over the golf ball (0.3 ± 0.3 min, $P < 0.001$) within the category balls. Within the category foraging enrichment, no preference for one over the other item was found ($P = 0.144$). Results of this study show that a hammock, conspecifics, foraging enrichment and a large water bowl are preferred enrichment options for ferrets.



## 1. Introduction

Ferrets (*Mustela putorius furo*) are commonly used for research purposes (e.g. influenza research) (Boyce et al., 2001) and are kept as pets, but research on behaviour and behavioural priorities of these animals is scarce (for a review, see Vinke and Schoemaker, 2012). It is believed that ferrets could benefit greatly from environmental enrichment (Fisher, 2006), which is demonstrated by their use of three-dimensional environments containing toys and multilevel shelves (Wolfensohn and Lloyd, 2003). In addition, ferrets used a barren cage 6–12 times less than any of three enriched cages in a preference test (Cruden, 2011). Moreover, ferrets in barren cages showed signs of stereotypic behaviour (bar chewing and head swaying) and quickly became lethargic, whereas the ferrets in an enriched isolation cage were active and curious and remained so throughout the study (Cruden, 2011).

The aforementioned studies did not investigate the preference and/or motivation for specific enrichment options. However, enrichments for which ferrets show a high motivation could possibly allow for performance of behavioural priorities and a lack of opportunity to do so could lead to the development of abnormal behaviour and stress (Jensen and Pedersen, 2008). This in turn is detrimental to animal welfare as well as the reliability of study results, as inter-individual variation might increase due to stress (e.g. Verwer et al., 2009). A validated method to assess the motivational strength and value of resources is measuring the price an animal is prepared to "pay" for (unlimited) access to these resources

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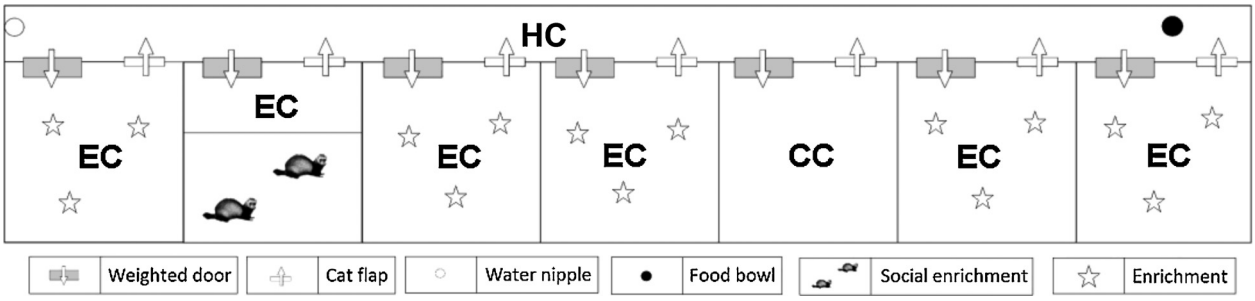


**Fig. 1.** Schematic representation of the experimental housing (HC = home corridor with a water nipple and food bowl, CC = control chamber, EC = enrichment chambers with, in randomised order, foraging enrichment, sleeping enrichment, tunnels, balls, conspecifics and water bowls).

(Cooper, 2004; Cooper and Mason, 2001; Mason et al., 1998). Such studies, referred to as consumer demand studies, involve imposing a strenuous task on the animal in order for it to gain access to a specific resource in a closed economy set-up. The task that the animal has to perform to gain access to the resource preferably involves an action that is considered a naturalistic task for the animal. Such a task requires the least amount of training and is also less prone to operant-reinforcer biases than unnatural tasks (Dawkins, 1990). In mink, a weighted door has been used for this purpose with success (Cooper and Mason, 2001).

By gradually increasing the effort that is needed to gain access to the resource, the maximum price paid (MPP) can be determined: the price at which the animal is no longer willing or able to perform the task. Compared to other indices used for measuring motivational strength, the MPP-index is believed to have the greatest internal validity (Houston, 1997), because 1) it is relatively insensitive to external cues (Warburton and Mason, 2003); 2) it can be applied to 'all-or-none' goods (Jensen and Pedersen, 2008; Olsson et al., 2002); and 3) an increase in price only has to be qualitative, so no assumptions about the subjective value of a task have to be made (Cooper, 2004).

Consumer demand studies often involve two-chamber set-ups that consist of a home chamber and one enrichment chamber in which the enrichments and an empty control are tested consecutively, as opposed to a three- or multi-chamber set-up, in which one or multiple resources and a control are tested concurrently. However, a recent study showed that a two-chamber set-up using a push door was unsuitable for ferrets, as they would push almost to their maximum push capacity for an empty compartment (Reijgwart et al., 2015). Thus, alternative set-ups (three- or multi-chamber) needed to be considered (e.g. Hovland et al., 2006; Mason et al., 2001; Seaman et al., 2008). In a three-chamber set-up, however, the enrichments are still tested consecutively, which might not solve the problems encountered in the two-chamber set-up. Therefore, a seven-chamber consumer demand study using a push door was used in this study to determine the maximum price ferrets paid for six enrichment categories (with different options per category) and one control chamber.

## 2. Animals and methods

### 2.1. Ethical note

This study was ethically approved by the Animal Care and Use Committee of Intravacc, Bilthoven, The Netherlands (DEC 201400137).

### 2.2. Animals, housing and husbandry

For the study, seven female, approximately 1 year old (range: 8–15 months), ferrets were used. Ferrets were obtained from Schimmel B.V., were surgically neutered (ovariectomized) at an age of 5 months and weighed 1011 ± 137 g at the moment of testing. Throughout the study, the ferrets were housed indoors in a room that was kept at a temperature between 19° C and 25° C. They were exposed to a 8:16 h light:dark schedule using artificial lighting (light bulbs) that switched on at 9:00 h and off at 17:00 h. In addition, auditory stimulation was available in the form of a radio to mask environmental noises, which automatically switched on and off concurrent with the light phase. Before and after the experiment, the ferrets were group-housed in phenolic faced plywood floor pens of 163 × 94 cm. In this pen, ferrets were provided with sawdust, a hiding place in the form of a flexible plastic bucket and *ad libitum* water (from a nipple) and food (Hope Farms® ferret balance pellets, Hope Farms, Woerden, the Netherlands). Refreshing of the food and water, as well as cleaning of the cages, took place daily at 9:30 am Prior to and throughout the study, the ferrets' health and overall condition were monitored on a daily basis.

### 2.3. Experimental housing

During the experiment, the ferrets were successively individually housed (24 h per day for a total of 26 days) in a closed economy, seven-chamber set-up consisting of one long corridor (692 cm long, 54 cm wide) connected to seven phenolic faced plywood floor pens (ground surface 107 × 94 cm; Fig. 1) with sawdust bedding. Between the corridor and each chamber, a 70 cm high, 6 mm thick phenolic faced plywood divider was present. The divider contained a wire mesh window through which the ferrets could see what was in the chamber, a non-transparent one-way cat flap (Petsafe® 4 Way Locking Deluxe Cat Flap, PetSafe, Ochten, The Netherlands); and a one-way horizontally hinged weighted door (Tecnilab-BMI, Someren, The Netherlands), similar to those used in the two-chamber study (Reijgwart et al., 2015). The weighted doors allowed the ferrets to move from the corridor, where *ad libitum* food and drinking water (via a nipple drinker) were provided, to the control chamber (CC), with only sawdust bedding, or the enrichment chambers (EC), where options from one of the enrichment categories (foraging toys, social contact, sleeping enrichment, water bowls, tunnels, balls) were placed in random order for each ferret. The one-way unweighted cat flaps, in contrast, could be used to return to the corridor. To push open the unweighted door, ferrets needed to exert a force of 200 g. Similar to the two-chamber study (Reijgwart et al., 2015), weights were added to the doors on a daily basis to gradually increase the effort needed to open the doors, starting with 250 g/day up to 1500 g, following which weights were increased with 125 g/day. The mechanism would transfer 50% of the added weight to the actual force needed for the ferret to open the door. Thus, a weight of 250 g translated to a push force of 325 g (200 + 50% of 250 g), a weight of 500 g to a push force of 450 g (200 + 50% of 500 g), etc. Under the doors, a wire mesh strip was

mounted to provide a traction surface for the ferrets to facilitate them to apply force to the doors.

### 2.4. Enrichments

Because environmental enrichment provides best results in terms of improvement of welfare if it is biologically relevant (i.e. improves biological functioning of the animal) (Newberry, 1995), enrichment categories were selected based on their relevance for enabling species-specific behaviours to be performed such as those seen in feral ferrets. i.e. foraging, sleeping, exploring, hunting, social interaction, drinking (Clapperton, 2001). In total, six enrichment categories were selected: 1) foraging enrichment, which enabled the animals to perform appetitive and consummatory behaviours; 2) sleeping enrichment, which provided the ferrets with a safe, dark place to sleep, similar to a burrow; 3) rigid and flexible tunnels, which provided the ferrets with play and exploration opportunities (Lloyd, 1999; Tynes, 2010); 4) balls, that were provided to stimulate the ferrets' hunting and capture behaviours, as well as play behaviour (Fisher, 2006); 5) social enrichment in the form of companionship of two familiar conspecifics; and 6) water bowls, which the ferrets could play in/with and allowed the ferrets to drink in a more natural way than from a nipple. (Table 1)

For each enrichment category, multiple options with different characteristics were offered to increase the likelihood of at least one of the options from the category being favoured by the ferrets. All ferrets were presented with the same range of enrichment options and the EC in which the options from each category were placed (cage order) was randomized for each ferret. With the exception of the sleeping bucket and conspecifics, none of the options had been previously provided to the ferrets. The conspecifics that were used as enrichment were randomly selected from the six ferrets that were not being tested at that moment and were housed behind mesh wire on sawdust, with a sleeping bucket, ad libitum food and a drinking bottle. Therefore, the ferrets could smell and hear each other, but had only limited opportunity for physical contact. In addition to the six enrichment categories, an empty cage was added as a seventh chamber that enabled to control for value of extra space, patrolling and the rewarding properties of interacting with the weighted door itself (Hansen et al., 2002). The six enrichment categories and the control chamber were allocated at random and the order was randomized for each ferret to control for chamber preferences.

### 2.5. Acclimatisation and training

The ferrets were already housed in the testing room and trained in using the weighted door for a previous experiment, in which their maximum push capacity (MPC) was determined using food as a reinforcer (1450 ± 144 g; Reijgwart et al., 2015). Each ferret was allowed to habituate to the experimental housing for seven days prior to commencing the experiment. In this period, all ferrets visited every chamber at least once and were therefore familiar with the enrichments in each chamber. During this period, doors were left unweighted and the enrichments were placed in EC to allow ferrets to enter and explore the enriched chambers without having to put in extra effort. After the acclimatisation period, weights were added to the doors on a daily basis over a period of 19 days until a weight of 3000 g was reached.

### 2.6. Maximum price paid

The maximum weight the ferrets were prepared to push (i.e. maximum price paid) for each of the enrichment categories and a control chamber were determined by daily increasing the effort needed to open the doors, while ensuring that all doors had similar weights added to the doors at all times. Ferrets were considered to have reached their maximum price paid (MPP) for a particular enrichment category when they did not visit the chamber containing that specific category for 24 h. MPP was subsequently determined as the last weight successfully pushed to gain access to EC and recorded in grams for each individual ferret and enrichment category. To identify which enrichment categories are most likely important to all ferrets and in which categories there are more individual preferences, standard deviations from the mean MPP and individual ranking of the MPP's are discussed.

### 2.7. Behavioural analyses

In addition to MPP, video recordings were made of the ferrets' activities in the experimental set-up. These recordings were used to score the number of times the ferrets entered the different chambers for each weight, as well as the time spent in each of the chambers. This was done by continuously scoring the video's and noting the time of day the ferrets entered a chamber through the weighted door and exited through the weighted cat flap in. For this purpose, the time of day that was displayed on the video footage (hh:mm:ss) was used. These data were used to validate the increasing weight as a cost. In addition, the ferrets' interactions with each of the individual options (except for the social enrichment) were evaluated in order to determine the ferrets' preferences for the options within an enrichment category and to investigate possible underlying motivations for the priorities and preferences of the ferrets. When a ferret made no visits to a resource at a specific weight, number of visits and mean visit duration were noted as missing data.

### 2.8. Statistical analysis

Analyses were performed using IBM SPSS Statistics for Windows, version 22.0

(IBM Corp., Armonk, N.Y., USA). Data are expressed as mean ± SD and the probability level accepted for statistical significance was $P < 0.05$ unless stated otherwise. Differences in MPP, order effects and changes in number and average duration of visits to the enrichment chambers with increasing weights were analysed using a Linear Mixed Model with enrichment category and weight on door as fixed effects and ferret ID as a random factor. Prior to running the analysis, normality of residuals and random intercept were tested to ensure that all required assumptions were met. A Paired Samples *T*-test (for the enrichment categories with two options) or 1-way ANOVA (for the enrichment categories with three options) was used to analyse differences in time spent with the enrichment options within an enrichment category. Normality of data and homogeneity of variances were tested and where appropriate, a nonparametric analysis was used. Individual ranking of the enrichment categories was done by assigning ranks 1–7 for the highest to the lowest MPP per individual ferret. When enrichment categories had the same MPP, they were assigned the same rank. The total, and average of these individual rankings were calculated.

## 3. Results

### 3.1. Maximum price paid

The maximum price paid by the ferrets to gain access to the different chambers differed significantly (LMM: $F_{36.000} = 10.030$, $P < 0.001$; Fig. 2). The chamber in which the enrichments were placed was not found to affect MPP for the different EC (LMM: $F_{36.000} = 0.827$, $P = 0.556$).

Findings demonstrated that the MPP for sleeping enrichment (1450 ± 120 g) was similar to the ferrets' MPC (1450 ± 144 g;

**Table 1**
Overview of the enrichments in each enrichment category. Numbers indicate the supplier of the enrichment, 1 = Van der Neut, Groenekan, The Netherlands, 2 = onlinedierenspeciaalzaak.com, 3 = Zooplus.nl, 4 = Tecnilab-BMI, Someren, The Netherlands 5 = Schimmel BV, The Netherlands.

| Enrichment category | Enrichments | Specifications |
|---|---|---|
| Foraging enrichment | Foraging ball | Happy Pet® tumble 'n treat, ø6 cm[1] |
| | Tumbler | Nina Ottoson Cat pyramid®, 9.5 cm high[2] |
| Sleeping enrichment | Bucket | Flexible plastic bucket[1] |
| | Savic Cocoon | Savic Cocoon®, 34.5 × 26.5 × 16.0 cm[1] |
| | Hammock | Adori® hammock, 50 × 45 cm[1] |
| Tunnels | Rigid tunnel | Ferplast® tunnel FPI 4840, ø10.5 cm, length 29 cm[1] |
| | Flexible tunnel | Zooplus® 260697.0, ø10 cm, length 19–75 cm[3] |
| Balls | Ball with bell | Cat play ball[1] |
| | Golf ball | ø4 cm |
| | Ferret ball | Ferret ball, ø25 cm, 4 holes ø10.2 cm[4] |
| Social enrichment | Conspecifics | Two familiar female ferrets[5] |
| Water bowls | Large bowl | Marchioro® kitten litterbox filled with water, 26 × 36 × 9 cm[1] |
| | Small bowl | Adori® stoneware food bowl filled with water, ø18 cm, 5 cm high[1] |

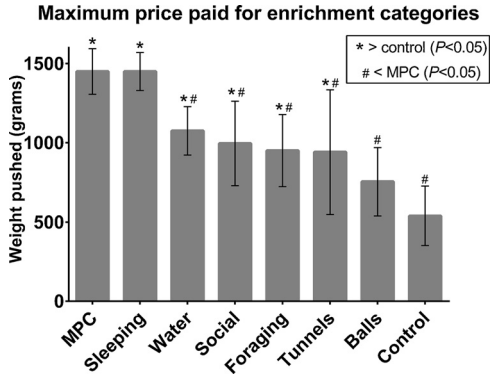


**Fig. 2.** Maximum price paid by neutered female ferrets (N = 7, mean ± SD) for the six different enrichment categories and a control.

**Table 2**
Total number of neutered female ferrets that ranked the seven categories 1–7 and average ranking of the enrichment categories.

| Enrichment Category | Ranking | | | | | | | Average |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| Sleeping enrichment | 6 | 1 | – | – | – | – | – | 1 |
| Water bowls | – | 4 | 1 | 1 | 1 | – | – | 3 |
| Social | 1 | 1 | 2 | 2 | 1 | – | – | 3 |
| Foraging enrichment | 1 | – | 2 | 3 | 1 | – | – | 3 |
| Tunnels | 1 | – | 1 | 3 | 1 | 1 | – | 4 |
| Balls | – | – | 1 | – | 2 | 2 | 2 | 6 |
| Control | – | – | – | – | 1 | 2 | 4 | 6 |

$P = 0.720$). Additionally, the MPP for sleeping enrichment was significantly higher than the MPP for all other enrichments and the CC ($P = 0.008$ for water bowls; $P = 0.001$ for social enrichment; $P < 0.001$ for all other comparisons). For four of the enrichment categories (water bowls: 1075 ± 153 g; social enrichment: 995 ± 267 g; foraging enrichment: 950 ± 228 g; tunnels: 940 ± 393 g), the MPP's were significantly higher than that for CC (539 ± 187 g; $P = 0.002$; 0.017; 0.005; 0.020, respectively). Only for the balls (754 ± 215 g) no significant differences were found when comparing its MPP with that for the CC ($P = 0.175$).

### 3.2. Individual differences in MPP

The SD in MPP was lowest for sleeping (120 g) and highest for tunnels (292 g) (Fig. 2). Additionally, sleeping enrichment was ranked the highest in all but one ferret and CC was ranked lowest or next-to-lowest in 6 out of 7 ferrets (Table 2). All other enrichments were ranked more variable by the individual ferrets (Table 2).

### 3.3. Validation of costs

The number of visits to the enrichment chambers declined upon increasing the weights on the door (LMM: $F_{917.000} = 43.722$, $P < 0.001$; Fig. 3a), while weight had no significant effect on the average visit duration (LMM: $F_{917.000} = 3.590$, $P = 0.058$; Fig. 3b).

### 3.4. Interaction with enrichment options

In addition to using the sleeping enrichment for its intended purpose (sleeping), the hammock and Savic Cocoon® were also used as tugging toy and hiding location for food and foraging enrichment, respectively. When comparing the different enrichments within this category, significant differences were observed in interaction times (Friedman df = 2, $P < 0.05$, Fig. 4), with interaction times with the hammock (9.2 ± 5.9 h) being significantly higher than that for the Savic Cocoon® (0.6 ± 0.8 h, $P = 0.011$).

The ferrets played with all types of balls, interaction with the balls consisted of pushing the balls forward, running or hopping after the balls and pouncing the balls. Occasionally, the ferrets were also observed to crawl through the holes in the ferret ball. Upon comparison of the interaction times with the different balls, significant differences were observed (Friedman: df = 2, $P = 0.021$, Fig. 4), with interaction times with the ferret ball (0.9 ± 0.5 min) being significantly higher than that with the golf ball (0.3 ± 0.3 min, $P = 0.003$).

The tunnels were mainly used to walk through. In addition, ferrets also used the tunnels as toys to push around. When comparing the different tunnels, interaction time with the flexible tunnel (6.1 ± 2.6 min) was higher than interaction time with the rigid tunnel (0.3 ± 0.2 min; Paired Samples *T*-Test: df = 6, $P < 0.001$, Fig. 4).

Most of the times, the ferrets used the foraging enrichment to directly obtain food from, which they achieved by pushing the items around. However, ferrets were also frequently observed to drag the enrichments out of EC and stash them elsewhere, most often the EC with sleeping enrichment and more specifically, the Savic Cocoon®. Upon comparing the different foraging enrichments, no significant differences were observed between the items (foraging ball: 4.2 ± 2.3 min; tumbler: 2.1 ± 1.6 min; Paired Samples *T*-Test: df = 4, $P = 0.114$, Fig. 4).

Despite the ferrets having free access to a drink nipple in the corridor, they were often found to use the water bowls as an alternative water source. In fact, as long as they gained access to the water bowls, they fully ceased using the drink nipple. Occasionally, the ferrets were found to play and display digging behaviours in the water bowls. Comparison of the different water bowls revealed interaction times with the large water bowl (5.8 ± 1.7 min) to be significantly higher than with the small water bowl (3.1 ± 0.8 min; Paired Samples *T*-Test: df = 6, $P = 0.014$, Fig. 4).

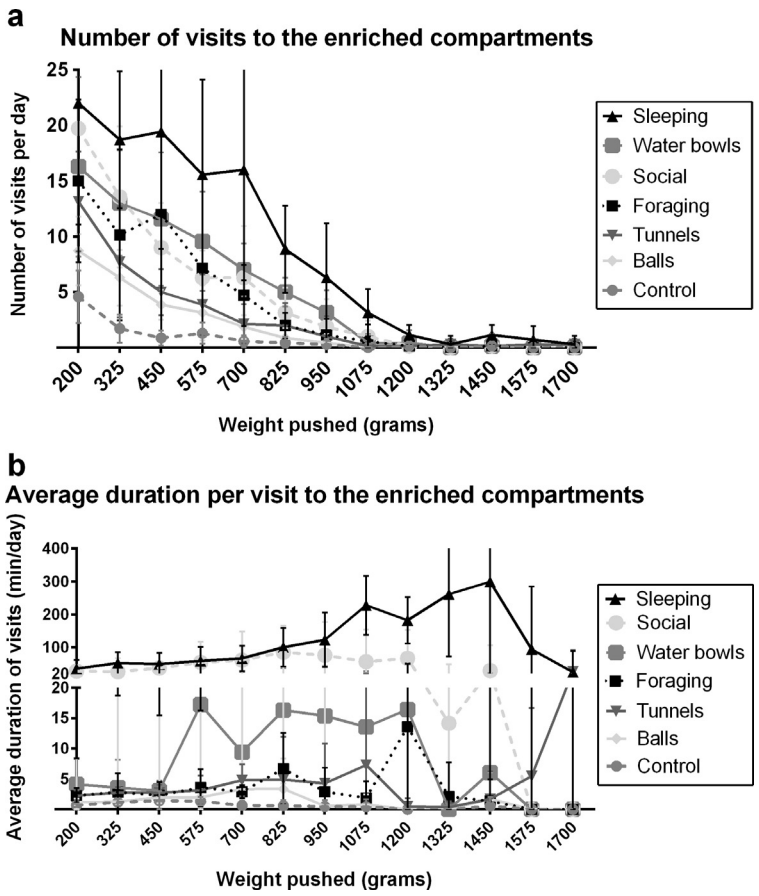


**Fig. 3.** Number of (a) and average duration per (b) (mean ± SD) visit to six different enrichment chambers (sleeping, water bowls, social, foraging, tunnels, balls) and a control chamber upon increasing the weight on the door by neutered female ferrets (N = 7).

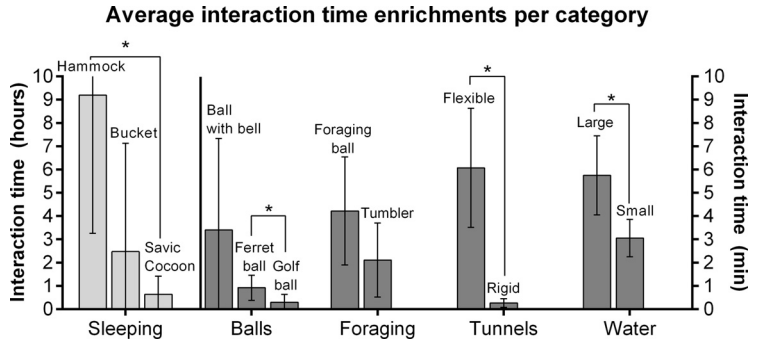


**Fig. 4.** Average interaction time (mean ± sd) with the enrichments in the five different categories (sleeping enrichment, balls, tunnels, foraging enrichment and water bowls) by neutered female ferrets (N = 7).

Evaluation of the type of interactions between the ferrets in the social enrichment revealed that, despite the inability to have direct contact, the ferrets would interact with the familiar conspecifics. The type of interaction seen mostly involved sleeping next to the mesh that separated them from their conspecifics. Occasionally, the ferrets would also perform short bouts of social play behaviour (weasel war dance, play invitation) towards the other ferrets. No aggressive or marking behaviour was seen. Upon the door weights exceeding 1 kg, a marked difference was observed in the ferrets' behaviour. Instead of going into the EC with social enrichment, they would sleep in the corridor next to the EC containing the familiar conspecifics, thereby allowing them direct visual contact with the other ferrets.

## 4. Discussion

The aim of this study was to evaluate the preferences and motivational strengths of ferrets for specific enrichments in a seven-chamber consumer demand study using a weighted push door. Based on the results for MPP, ferrets were found to work harder to gain access to sleeping enrichment than for any of the other enrichment categories. In addition, inter-individual differences in motivation for sleeping enrichment were the smallest, with all but one ferret being motivated the most to gain access to the sleeping enrichments.

Ferrets furthermore put significantly more effort in gaining access to social enrichment, water bowls, foraging enrichment and tunnels compared to an empty control chamber. However, inter-

individual differences in motivation for these enrichments were higher than for sleeping enrichment (i.e. some ferrets were highly motivated to gain access to these enrichment categories, while others were not), with inter-individual variation being highest for tunnels.

Of the six enrichment categories provided, ferrets showed the least motivation to gain access to the balls, with no significant differences found between this enrichment category and the control chamber.

### 4.1. Sleeping enrichment

The high motivation for the sleeping enrichments was expected, as laboratory ferrets sleep 60–70% of the time (Jha et al., 2006; Marks and Shaffery, 1996). The distinct preference for the hammock compared to the other sleeping enrichments was surprising, however, as biological data suggests that feral ferrets in the wild are mostly nocturnal and sleep in areas with cover during the day (Clapperton, 2001). Similarly, others have reported ferrets to prefer sleeping in dark, enclosed areas (Lloyd, 1999). However, other authors have anecdotally suggested a preference for hammocks as a resting site in pet ferrets (Tynes, 2010), as was demonstrated in our study. Possibly, the soft lining of the hammock mimics physical contact with conspecifics, which was another enrichment category the ferrets showed high motivation for and where the ferrets spent a large proportion of the time sleeping (as reflected in the long visit duration). This warrants further investigation, however, as there might be other explanations for the preference for the hammock, such as the rocking motion, warmth due to the soft material, space (the hammock is a 'second floor') or the snugness of the hammock.

### 4.2. Social enrichment

The high motivation for social interaction is in accordance with the observation that domesticated ferrets are gregarious and will sleep together, share food and water and play vigorously (Fisher, 2006; Lloyd, 1999). In addition, Warburton and Mason (2003) found that mink (*Mustela vison*), a close relative of the ferret with similar biologic characteristics, worked to gain access to conspecifics from which they were separated by a wired fence. An alternative hypothesis might be that the ferrets were highly motivated to visit the social chamber in order to gather information on the potential competitors in their territory (Chang et al., 2000; Takahashi, 1991). This explanation seems less likely, however, given the fact that the ferrets had been housed together previously with no fights occurring during this time. In addition, territorial behaviour might have been reduced by the ovariectomy (Takahashi, 1991). Moreover, if territoriality would play a role, interaction with the other ferrets would likely only involve awake and marking behaviours rather than sleeping in proximity of the other ferrets, which all ferrets did. Therefore, it is more likely that the visits to the conspecifics were social behaviour instead of territorial behaviour.

### 4.3. Water bowls

During our study, we found ferrets to be highly motivated to gain access to water bowls, a motivation they share with mink, which showed a preference for access to a swimming bath that was 60 cm deep (Mason et al., 2001). This is surprising, however, as the two species have different hunting territories. Whereas semi-aquatic mink hunt predominantly in the water (Dunstone and Davies, 1993), ferrets are primarily known as ground hunters that are rarely seen swimming (Clapperton, 2001). The ferrets in our study mainly used the water bowls as an alternative source of drink water, but as the water in the bowls in our study was too shallow to swim in, it is impossible to determine whether swimming was not observed as a result of the study design or whether ferrets really lack motivation to swim. Despite this limitation, we can conclude that ferrets prefer drinking from a bowl opposed to a nipple, as they were motivated to push to gain access to the water bowls even though the water nipple was freely available. Similar results have been found in other animal species, potentially because the water bowl allows for a more natural way of drinking e.g. (Tschudin et al., 2011). However, the water bowls also induced play behaviour (scratching) and may even be used for thermoregulation, therefore warranting further investigation in order to draw definitive conclusions about the underlying reasons for the high motivation for water containers. Similarly, the study design does not allow for conclusions to be drawn regarding the underlying reason for the preference for the larger, plastic litter box over the smaller, stoneware bowl, as both size and type of material differed between the two bowls. However, despite the small difference in interaction times being statistically significant, the biological relevance of this difference appears to be questionable given its small size.

### 4.4. Foraging enrichment

Aside from the sleeping enrichment, social contact and water bowls, ferrets also showed high motivation to gain access to foraging enrichment. This finding in itself is not surprising as many animals are observed to be willing to put in an extra effort to obtain food. The observation that the ferrets worked (pushed the heavy door) to work (roll the ball or tumbler) for food, while freely accessible food was available in the home corridor, can be explained by a concept called contrafreeloading, which states that working for food can be inherently enriching (Inglis et al., 1997). Foraging enrichment is considered to have great value to an animal, as it enables the animal to perform its natural foraging and feeding behaviours, one of the most essential behavioural patterns for survival (Newberry, 1995). The ferrets could perform natural hunting behaviour (i.e. stalking, catching and eating) using the foraging ball and tumbler, which also were small enough to pick up and drag elsewhere. Mustelids have been reported to cache their food (Macdonald, 1976) and ferret owners report food and item caching, so these foraging enrichments might also satisfy the tendency to cache food in a secluded area (in our study the Savic Cocoon®). Since both items were made of similar materials, contained the same reward and were light enough for the ferrets to carry around, both may have been equally attractive to the ferrets, thereby explaining the lack of a preference for one over the other.

### 4.5. Balls

As the golf ball, ferret ball and the ball with bell could only fulfil the appetitive part of the hunting sequence and because these enrichments were tested concurrently with foraging enrichment (which could fulfil the appetitive as well as the consummatory part of the hunting sequence and allowed for stacking food away from the food bowl), it is not surprising that the ferrets would stop visiting the EC with balls at low weights. In line with this, the ferrets preferred the ball with the bell within the category balls, which had a novel feature (the sound of the bell) and was the only ball could be picked up with the mouth. The differences in interaction time with the three types of balls were small, however, so the found differences, despite being statistically significant, may not be biologically relevant. Interestingly, none of the ferrets ever carried the ball with the bell out of the EC, as they did do with the foraging enrichments. Possibly, the need for caching food/items was already met using the foraging enrichments, which made it less worth wile to put in the effort to stash the ball.

### 4.6. Tunnels

Tunnels were also among the options for which ferrets were willing to put in effort to gain access to, even though individual variation in motivation was high for this enrichment. Considering the fact that feral ferrets' sleep in rabbit burrows and their main hunting grounds consists of rabbit tunnels (Clapperton, 2001), the high motivation for tunnels is not surprising as walking through a tunnel could readily help to mimic this behaviour. The preference for the opaque flexible tunnel over the rigid see-through tunnel is in line with the ferrets' preference for enrichment that mimics more natural circumstances, as rabbit holes are dark and usually do not follow a straight line. Moreover, the lighter, flexible tunnel provided an opportunity for ferrets to manipulate, drag and play with the tunnel, behaviours they were found to display also with the other items.

### 4.7. Limitations of the study

Unfortunately, the fundamental reasons behind the preferences for certain options within the categories can only be guessed, as this study was not designed to investigate which characteristics of the enrichments are most appealing to ferrets. Moreover, enrichment options will rarely serve a single function, which makes it difficult to choose options that only fit in one single category. However, the behavioural observations performed during this study may provide some indication regarding the enrichment's functionalities for the ferrets. Similarly, these limitations highlight the importance of testing multiple options within an enrichment category to obtain more reliable results regarding the value of a specific enrichment category. Choosing a single option to represent a specific category may pose a risk of drawing incorrect conclusions regarding the value of this category when an option is chosen that is not of interest to the ferret. In light of this, inter-individual preferences or aversion for specific options or conspecifics should also be taken into consideration, especially for categories for which a large inter-individual variation in motivation was found. Inter-individual variation can arise due to sex, life history, age and reproductive state, e.g. Vasconcellos et al., 2009. In this study, the sex, reproductive state and life histories of the ferrets were equal, but only one ferret could be tested at a time, which caused an age difference of 5.5 months between the first and the last ferret that was tested. However, the largest differences in motivation were not always found in the ferrets with the largest age differences, thus rendering it less likely for age to be a (sole) contributing factor in the animal's motivation for a resource. A large inter-individual variation may just as well indicate that those options are less important for the ferrets in general, therefore being more prone to individual preferences, whereas essential behavioural priorities are equally important to all ferrets, therefore resulting in high MPPs with little inter-individual variation.

Only female ferrets were used in this study, as male ferrets are less commonly used in animal studies. This comes with the advantage of less variability due to sex (as stated in the previous paragraph), but has the disadvantage that the results are not generalizable to male ferrets.

Test conditions may also be of influence on the results that were found. For example, motivation for and interaction with enrichments has been found to change when animals are tested when housed socially in groups (Elmore et al., 2011; Mench and Stricklin, 1990; Pedersen et al., 2002; Sherwin and Nicol, 1998). In addition, motivation to work for full social contact may be different from that for limited (vocal and visual) contact, as we evaluated in our study. In further studies, it would therefore be of interest to investigate the effects of social housing and access to full physical contact on the ferrets' preferences for different enrichments. The priorities and preferences of the ferrets were furthermore tested in a multi-chamber (seven-chamber) set-up, as a two-chamber set-up proved to be unsuitable for ferrets. However, a multi-chamber set-up can lead to interpretative problems due to animals abandoning resources at a different rate (Kirkden and Pajor, 2006). If one resource is abandoned, the value of the remaining resources might change because of the unavailability of the abandoned resource. In addition, an animal only has limited income (i.e. the time and energy available per day) which it needs to divide between the different resources if offered simultaneously as is the case in a multi-chamber consumer demand study, thereby potentially yielding lower MPP values for resources that are deemed less important to the animal. Especially if enrichment options are – in part – substitutes and allow for performance of similar behaviours to be performed (e.g. balls and foraging enrichment both allow appetitive behaviour), animals may choose the option that is most preferred, despite the other option being of interest to the animal as well. Thus, concurrent testing of (substitutable) resources might have caused erroneously low MPPs for some of the (less important) enrichment categories. It would therefore be important to also test the ferrets in a (3-chamber) set-up where they would not be offered the different options simultaneously to prevent them from having to choose and divide their time.

## 5. Conclusion

This study showed that, in a closed economy, seven-chamber consumer demand set-up, ferrets were motivated highest to gain access to a chamber containing sleeping enrichment, as represented by the high MPP, and long, frequent visits to this chamber. In addition, ferrets' motivation for social enrichment, water bowls, foraging enrichment and tunnels was also higher than for the chamber containing balls or the control chamber. For these enrichments, inter-individual variation was higher than for sleeping enrichment and inter-individual variation for tunnels was highest, indicating that ferrets may value these resources differently. Within the highest ranking categories (sleeping enrichment, social contact, water bowls, foraging enrichment and tunnels), ferrets were found to prefer the hammock, large water bowl and flexible tunnel, whereas no clear preference was found for either of the foraging enrichments. These preferences should be taken into account so that a captive living environment can be created that is optimally adjusted to the ferrets' preferences and behavioural priorities.

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## References

Boyce, S., Zingg, B., Lightfoot, T., 2001. Behavior of *Mustela putorius furo* (the domestic ferret). Vet. Clin. North Am. Exot. Anim. Pract. 4, 697–712.

Chang, Y.-M., Kelliher, K.R., Baum, M.J., 2000. Steroidal modulation of scent investigation and marking behaviors in male and female ferrets (*Mustela putorius furo*). J. Comp. Psychol. 114, 401, http://dx.doi.org/10.1037/0735-7036.114.4.401.

Clapperton, B., 2001. Advances in New Zealand mammalogy 1990–2000: feral ferret. J. R. Soc. N. Z. 31, 185–203, http://dx.doi.org/10.1080/03014223.2001.9517647.

Cooper, J., 2004. Consumer demand under commercial husbandry conditions: practical advice on measuring behavioural priorities in captive animals. Anim. Welf. 13, 47–56.

Cooper, J.J., Mason, G.J., 2001. The use of operant technology to measure behavioral priorities in captive animals. Behav. Res. Methods Instrum. Comput. 33, 427–434, http://dx.doi.org/10.3758/BF03195397.

Cruden, J., 2011. Improvement and refinements in husbandry processes and environmental enrichment for ferrets housed at CL III levels of containment. Anim. Technol. Welf. 10, 177.

Dawkins, M.S., 1990. From an animal's point of view: motivation, fitness, and animal welfare. Behav. Brain Sci. 13, 1–9, http://dx.doi.org/10.1017/S0140525X00077104.
Dunstone, N., Davies, J., 1993. The Mink. Poyser, London.
Elmore, M.R.P., Garner, J.P., Johnson, A.K., Kirkden, R.D., Richert, B.T., Pajor, E.A., 2011. Getting around social status: motivation and enrichment use of dominant and subordinate sows in a group setting. Appl. Anim. Behav. Sci. 133, 154–163, http://dx.doi.org/10.1016/j.applanim.2011.05.017.
Fisher, P.G., 2006. Chapter 4 - ferret behavior. In: Mayer, T.B.B.L. (Ed.), Exotic Pet Behavior. W.B. Saunders, Saint Louis, pp. 163–205, http://dx.doi.org/10.1016/B978-1-4160-0009-9.50011-6.
Hansen, S.W., Jensen, M.B., Pedersen, L.J., Munksgaard, L., Ladewig, J., Matthews, L., 2002. The type of operant response affects the slope of the demand curve for food in mink. Appl. Anim. Behav. Sci. 76, 327–338, http://dx.doi.org/10.1016/s0168-1591(02)00008-4.
Houston, A.I., 1997. Demand curves and welfare. Anim. Behav. 53, 983–990, http://dx.doi.org/10.1006/anbe.1996.0397.
Hovland, A.L., Mason, G., Bøe, K.E., Steinheim, G., Bakken, M., 2006. Evaluation of the 'maximum price paid'as an index of motivational strength for farmed silver foxes (*Vulpes vulpes*). Appl. Anim. Behav. Sci. 100, 258–279, http://dx.doi.org/10.1016/j.applanim.2005.11.006.
Inglis, I.R., Forkman, B., Lazarus, J., 1997. Free food or earned food? A review and fuzzy model of contrafreeloading. Anim. Behav. 53, 1171–1191, http://dx.doi.org/10.1006/anbe.1996.0320.
Jensen, M.B., Pedersen, L.J., 2008. Using motivation tests to assess ethological needs and preferences. Appl. Anim. Behav. Sci. 113, 340–356, http://dx.doi.org/10.1016/j.applanim.2008.02.001.
Jha, S.K., Coleman, T., Frank, M.G., 2006. Sleep and sleep regulation in the ferret (*Mustela putorius furo*). Behav. Brain Res. 172, 106–113, http://dx.doi.org/10.1016/j.bbr.2006.05.001.
Kirkden, R.D., Pajor, E.A., 2006. Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. Appl. Anim. Behav. Sci. 100, 29–47, http://dx.doi.org/10.1016/j.applanim.2006.04.009.
Lloyd, M., 1999. Ferrets: health, husbandry and diseases. Blackwell Sci., http://dx.doi.org/10.1016/b978-0-7020-2827-4.50009-7.
Macdonald, D.W., 1976. Food caching by red foxes and some other carnivores. Zeitschrift für Tierpsychologie 42, 170–185, http://dx.doi.org/10.1111/j.1439-0310.1976.tb00963.x.
Marks, G.A., Shaffery, J.P., 1996. A preliminary study of sleep in the ferret, *Mustela putorius furo*: a carnivore with an extremely high proportion of REM sleep. Sleep 19, 83–93.
Mason, G., McFarland, D., Garner, J., 1998. A demanding task: using economic techniques to assess animal priorities. Anim. Behav. 55, 1071–1075, http://dx.doi.org/10.1006/anbe.1997.0692.
Mason, G.J., Cooper, J., Clarebrough, C., 2001. Frustrations of fur-farmed mink. Nature 410, 35–36, http://dx.doi.org/10.1038/35065157.
Mench, J.A., Stricklin, W., 1990. Consumer demand theory and social behavior: all chickens are not equal. Behav. Brain Sci. 13, http://dx.doi.org/10.1017/s0140525x00077323 (28–28.).
Newberry, R.C., 1995. Environmental enrichment: increasing the biological relevance of captive environments. Appl. Anim. Behav. Sci. 44, 229–243, http://dx.doi.org/10.1016/0168-1591(95)00616-Z.
Olsson, I., Keeling, L., McAdie, T., 2002. The push-door for measuring motivation in hens: an adaptation and critical discussion of the method. Anim. Welf. 11, 1–10, http://dx.doi.org/10.1016/j.applanim.2010.12.008.
Pedersen, L.J., Jensen, M.B., Hansen, S.W., Munksgaard, L., Ladewig, J., Matthews, L., 2002. Social isolation affects the motivation to work for food and straw in pigs as measured by operant conditioning techniques. Appl. Anim. Behav. Sci. 77, 295–309, http://dx.doi.org/10.1016/s0168-1591(02)00066-7.
Reijgwart, M.L., Vinke, C.M., Hendriksen, C.F.M., van der Meer, M., Schoemaker, N.J., van Zeeland, Y.R.A., 2015. Workaholic ferrets: does a two-chamber consumer demand study give insight in the preferences of laboratory ferrets (*Mustela putorius furo*)? Appl. Anim. Behav. Sci. 171, 161–169, http://dx.doi.org/10.1016/j.applanim.2015.08.032.
Seaman, S.C., Waran, N.K., Mason, G., D'Eath, R.B., 2008. Animal economics: assessing the motivation of female laboratory rabbits to reach a platform, social contact and food. Anim. Behav. 75, 31–42, http://dx.doi.org/10.1016/j.anbehav.2006.09.031.
Sherwin, C., Nicol, C., 1998. A demanding task: using economic techniques to assess animal priorities a reply to Mason et al. Anim. Behav. 55, 1079–1081, http://dx.doi.org/10.1006/anbe.1997.0694.
Takahashi, L.K., 1991. Hormonal regulation of sociosexual behavior in female mammals. Neurosci. Biobehav. Rev. 14, 403–413, http://dx.doi.org/10.1016/s0149-7634(05)80062-4.
Tschudin, A., Clauss, M., Codron, D., Hatt, J., 2011. Preference of rabbits for drinking from open dishes versus nipple drinkers. Vet. Rec. 168, 190, http://dx.doi.org/10.1136/vr.c6150.
Tynes, V.V., 2010. Behavior of Exotic Pets. John Wiley & Sons.
Vasconcellos, A., Guimaraes, M., Oliveira, C.A.d, Pizzutto, C.A.d., Ades, C.S., 2009. Environmental enrichment for maned wolves (*Chrysocyon brachyurus*): group and individual effects. Anim. Welf. 18, 289–300.
Verwer, C.M., van der Ark, A., van Amerongen, G., van den Bos, R., Hendriksen, C.F.M., 2009. Reducing variation in a rabbit vaccine safety study with particular emphasis on housing conditions and handling. Lab. Anim. 43, 155–164, http://dx.doi.org/10.1258/la.2008.007134.
Vinke, C.M., Schoemaker, N.J., 2012. The welfare of ferrets (*Mustela putorius furo T*): a review on the housing and management of pet ferrets. Appl. Anim. Behav. Sci. 139, 155–168, http://dx.doi.org/10.1016/j.applanim.2012.03.016.
Warburton, H., Mason, G., 2003. Is out of sight out of mind? The effects of resource cues on motivation in mink *Mustela vison*. Anim. Behav. 65, 755–762, http://dx.doi.org/10.1006/anbe.2003.2097.
Wolfensohn, S., Lloyd, M., 2003. Carnivores. In: Wolfensohn, S., Lloyd, M. (Eds.), Handbook of Laboratory Animal Management and Welfare, Blackwell Publishing Ltd, Oxford. , pp. 281–303, http://dx.doi.org/10.1002/9780470751077 (chapter 14).