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Workaholic ferrets: Does a two-chamber consumer demand study give insight in the preferences of laboratory ferrets (*Mustela putorius furo*)?

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ABSTRACT

Although provision of environmental enrichment is an effective tool to refine laboratory animal experiments, it is currently unknown which enrichments ferrets prefer. This study aimed to assess the suitability of a closed economy, two-chamber consumer demand set-up to determine ferrets' preferences for selected enrichments. Twelve female ferrets were housed in a set-up consisting of a home and enrichment chamber (EC) connected by a weighted door. The maximum weights the ferrets pushed for food (MPP_{food}) and an empty chamber (MPP_{empty}) were determined to evaluate the maximum push capacity of the animals and as a control. Although the ferrets pushed significantly more for food (1325 ± 213 g) than for the empty chamber (1169 ± 193 g), the weight difference was minor (MPP_{empty} was 89 ± 13% of MPP_{food}). To evaluate the ferrets' underlying motivation to push for the empty chamber, a second study was performed in which MPP_{empty} was tested in seven alternative set-ups. The first three set-ups included adapted versions of the standard design (set-up A_1, A_2 and A_3), intended to determine the functional value of the empty chamber. The four other set-ups (set-up B_0, B_1, B_3, B_4) aimed to evaluate the attractiveness of the door elements by allowing the ferrets to choose whether or not to use the weighted door to enter EC. Results demonstrated no significant differences in MPP_{empty} between the A-set-ups, indicating that the value of the empty chamber could not be reduced by adapting the set-up. MPP_{empty} reduced when allowing the ferrets free access to EC, demonstrating that the empty chamber had reinforcing properties. Nevertheless, the ferrets were still motivated to use the weighted door despite being granted free access to EC, indicating that the door also has reinforcing properties. The ferrets decreased the use of the weighted door most when, in a set-up with free access to EC, the nest box in the home cage (53 ± 22% of MPP_{food}) was replaced by a manipulable plastic bucket (26 ± 13% of MPP_{food}). These results indicate that availability of items in the home chamber may influence the results, which should be taken into account when designing motivation studies similar to the one performed in this study. The lack of differences between MPP_{food} and MPP_{empty} furthermore demonstrates that the two-chamber set-up is not suitable for evaluating the ferrets' motivation for enrichments, thus necessitating other alternatives, such as a three- or multi-chamber consumer demand study, to be explored.

1. Introduction

Ferrets (*Mustela putorius furo*) are commonly used for research purposes (e.g. influenza research) (Boyce et al., 2001). To ensure humane use of laboratory animals, the principles of reduction, replacement and refinement (the three R's) are employed (Russell et al., 1959). Refinement includes the optimization of the animal's housing conditions, e.g. by providing environmental enrichment

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(Russell et al., 1959). Environmental enrichment can improve animal welfare at least to a certain degree by providing some of the appropriate stimuli needed to perform species-specific behaviour (Newberry, 1995).

Traditionally, the preference for alternative resources is assessed in preference tests, in which the animal is given a two-way unweighted choice between alternative resources. One preference test with ferrets indicated that these animals prefer an enriched over a barren cage, but did not specify which enrichments are preferred (Cruden, 2011). Unfortunately, these preference tests only address the relative rather than the actual value of the enrichment (Kirkden and Pajor, 2006). In other words, they assess whether animals 'like' (affective consequence) a specific enrichment item and not whether they 'want' (are motivated to access) this item (Berridge and Robinson, 2003).

To address the actual value of a specific enrichment item, so-called consumer demand studies may be used. Such studies have been used extensively in various laboratory and production animals, including mice (Sherwin, 1996), rats (Manser et al., 1996, 1998; Patterson-Kane et al., 2002), silver foxes (Hovland et al., 2006) and mink (Mason et al., 2001). A consumer demand study comprises a set-up in which increasing costs are imposed on the animal in order for it to gain access to a specific resource.

The value of the enrichment can be expressed using various indices, including the price elasticity of demand index, the consumer surplus index and the maximum price paid index (Kirkden et al., 2003). The maximum price paid (MPP) index indicates the 'breakpoint' at which the animal is no longer willing to pay the price for the resource. This index has several advantages over the other indices, including a) its relative insensitivity to external cues (Warburton and Mason, 2003); b) its usefulness for the testing of 'all-or-none' goods (Olsson et al., 2002); and c) the possibility to use qualitative rather than quantitative increases in price, thereby omitting the need to make assumptions about subjective value of a task (Cooper, 2004). As a result, the MPP index is generally preferred for analyzing the value of resources.

To infer information on the actual value of a resource, MPP is tested consecutively for various resources, including food (MPP_{food}, which is considered to reflect the maximum amount of weight an animal is able to push: the maximum push capacity), an empty chamber (MPP_{empty}, which serves as a control) and the different enrichment items (e.g. Asher et al., 2009). Most commonly, testing takes place in a closed economy two-chamber set-up, i.e. the animals are housed permanently in the experimental set-up. This prevents the animals from becoming less motivated to work for a resource because of its (free and/or unlimited) access to the item outside of the experimental set-up (Jensen and Pedersen, 2008; Ladewig et al., 2002). Animals have also been tested in three- or multiple-chamber designs, in which they can simultaneously gain access to one or multiple resources and a control (e.g. Hovland et al., 2006; Mason et al., 2001; Seaman et al., 2008). These set-ups, however, introduce an extra variable, as the animal only has limited income (i.e. the time and energy available per day) which it then needs to divide between the different resources, thereby potentially yielding lower MPP values for resources that are less important.

As no consumer demand studies have been performed in ferrets thus far, the current study focused on establishing the functionality of a two-chamber consumer demand study in ferrets using the MPP index. Similar to the consumer demand study with mink (Mason et al., 2001), a weighted door was used. To be considered suitable for testing the ferrets' motivation for resources, the experimental set-up needs to meet three prerequisites: (1) MPP_{food} should reflect the maximum push capacity (MPC); (2) the task should be perceived as strenuous and (3) MPP_{empty} should be low and sufficiently distinctive from MPP_{food}. To assess whether these prerequisites were met, MPP_{food}, MPP_{empty} and duration and number of visits to the chamber with food and to an empty chamber were measured. As ferrets were found to push excessively for an empty room (i.e. the third prerequisite was not met), two subsequent studies were performed to assess how and which features of the design may have affected MPP_{empty}.

2. Animals, materials and methods

2.1. Ethical approval

This study was ethically approved by the Institutional Animal Care and Use Committee of Intravacc (DEC 201300057) and Utrecht University (DEC 2013.I.09.073).

2.2. Animals

For study 1, 12 female neutered ferrets from Schimmel B.V. were used that weighed 1.0 ± 0.2 kg (665–1145 g). Six ferrets were 4 years old and chemically neutered using a hormonal implant (Suprelorin®, Virbac, The Netherlands); the other six ferrets were 5 months old and surgically neutered (ovariectomized). For study 2, five of the 4-year-old female ferrets from study 1 were used. These ferrets weighed 838 ± 113 g (665–938 g).

2.3. Housing and nutrition

Ferrets were housed indoors in a room that was kept at a temperature between 18 °C and 22 °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, which automatically switched on and off concurrent with the light phase. The ferrets were provided water and food (Hill's M/D® for the 4-year old ferrets, Hope Farms® ferret balance pellets for 5-month-old ferrets) ad libitum. Refreshing of the food and water, as well as cleaning of the cages took place daily at 10:00 h. The ferrets' health and overall condition were monitored prior to and throughout the study.

2.4. Experimental housing

Throughout the experiments, the ferrets were individually housed in a closed economy two-chamber set-up consisting of a phenolic faced plywood floor pen with solid floors and walls that measured 1.6 m^2 (Fig. 1a). The pens were divided in two equal spaces by means of a 70 cm high, 6 mm thick phenolic faced plywood divider equipped with a non-transparent one-way cat flap and a one-way horizontal swinging weighted door (Tecnilab-BMI, Someren, The Netherlands; Fig. 1b). Under the door, a wire mesh strip was mounted to provide a traction surface for the ferrets to facilitate them to apply force to the door. The door allowed the ferrets to move from a home chamber (HC) equipped with a resting area (i.e. nest box or plastic sleeping bucket), food (except when testing MPP_{food}) and water (provided via a nipple) to the enrichment chamber (EC) where the resource to be tested (e.g. food, enrichment) was placed. The one-way unweighted cat flap could subsequently be used by the ferrets to return to HC.

2.5. Task

Similar to mink (Cooper and Mason, 2001), ferrets had to push a weighted door, which is considered as a naturalistic task for ferrets that requires little training and is less prone to operant-reinforcer biases than unnatural tasks (Dawkins, 1990). To open the unweighted door, ferrets needed to exert a force of 200 g. Similar to mink, the force needed to push open the door was gradually

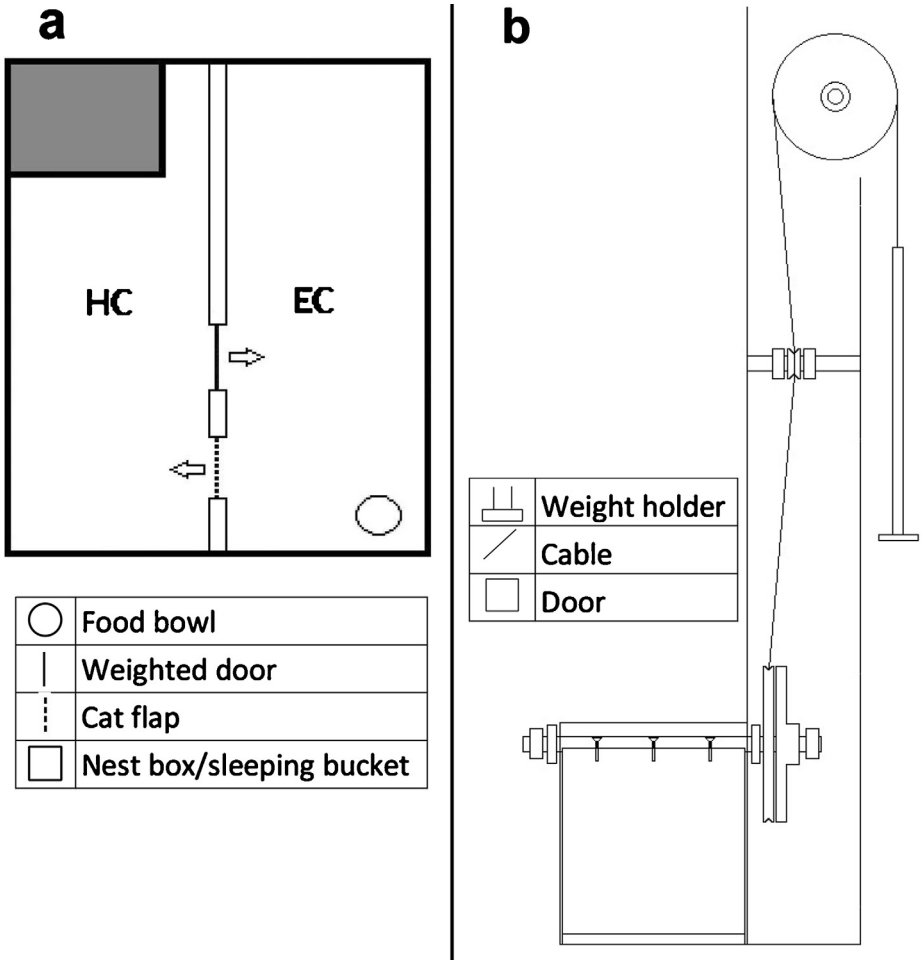

Fig. 1. (a) Layout of design A_0 (study 1, $N = 12$). HC = home chamber; EC = enrichment chamber; arrows indicate the direction in which the ferrets could pass through the cat flap or weighted door. (b) Drawing of the door mechanism; weights could be added to a cable that was connected to the door via three pullies, thereby increasing the effort needed to open the door to gain access to EC.

increased by adding 250 g of weight to the door mechanism each consecutive day (Mason et al., 2001). 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.

2.6. Acclimatization and training

The ferrets were allowed to acclimatize to their experimental housing for 14 days prior to initiating the training. During this period, the animals were encouraged to visit both chambers by placing food in EC and providing free access to both rooms by leaving the cat flap and door open. In the 3rd week, the ferrets were trained to use the door and the cat flap by gradually closing both doors over a period of 4 days, necessitating the ferrets to push the door open further each day to gain access to the other room. As the ferrets readily used the doors, no additional training was required.

Prior to commencing the experiments, the ferrets were allowed free access to both sides for another 3 days. Once they had used both doors and accessed both rooms for 3 consecutive days, the experiment commenced.

2.7. Study 1 – suitability of the design

Study 1 was designed to test whether the current design met the three prerequisites needed to demonstrate suitability of the design to evaluate motivation for different resources (i.e. (1) $MPP_{food} = MPC$; (2) the task is strenuous; (3) $MPP_{empty} < MPP_{food}$).

The first prerequisite ($MPP_{food} = MPC$) was tested by having the ferrets work for food in the standard set-up (A_0). Since food passage time in ferrets is approximately 3 h (Bleavins and Aulerich, 1981), ferrets were expected to be motivated to gain access to the food in EC at least once per 24 h. Ferrets were considered to have reached their maximum price paid for food (MPP_{food}) when they did not visit EC for 24 h. MPP_{food} was subsequently recorded as the last weight successfully pushed to gain access to food. The ferrets were monitored through 24-h video recordings to see whether they attempted to push the door above their MPP_{food} but were unable to succeed or stopped pushing the door altogether, thereby confirming that MPP_{food} indeed equalled MPC.

The second prerequisite (pushing the door is a strenuous task) was tested by evaluating whether changes in the number and duration of visits occurred upon increasing the effort to gain access to EC. The task should be demanding as a task that is fun or easy will result in ferrets pushing the door merely just for the act of pushing rather than gain access to the resources provided in EC. If the task is demanding, the number of visits should decline and the duration of visits is expected to increase with increasing weights to keep consumption of the resource constant at the lowest possible daily total price, as has been observed in other studies (Cooper, 2004; Sherwin and Nicol, 1996).

The third prerequisite ($MPP_{empty} < MPP_{food}$) was tested by determining the weight the ferrets were willing to push to gain access

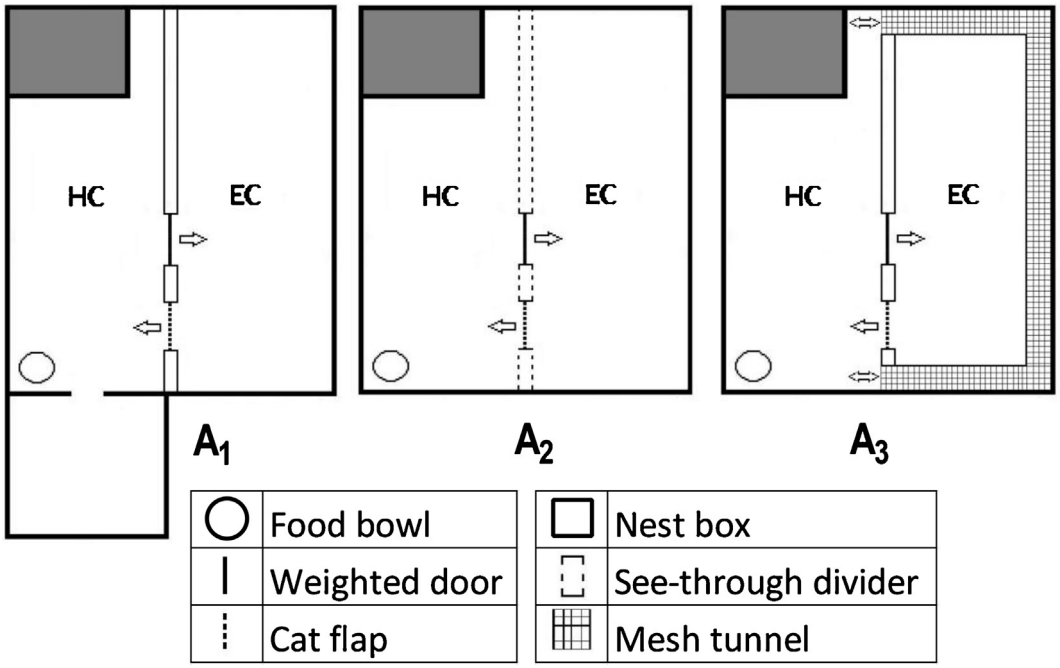

Fig. 2. The three set-ups that were used in study 2a. Set-ups were similar to the original design in study 1, but included (a) an extra chamber (A_1); (b) a see-through divider rather than a wooden divider (A_2); and (c) a mesh tunnel that allowed the ferret to explore the perimeters of the empty chamber without it having to push the door (A_3). Arrows indicate the way the ferrets can pass through the cat flap or weighted door.

to an empty chamber (MPP_{empty}). For this purpose, the food was moved back to HC after which 250 g of weight was added to the door on a daily basis. Similar to MPP_{food}, MPP_{empty} was determined as the last recorded weight at which the ferrets pushed the weighted door to gain access to EC within a 24-h time frame.

2.8. Study 2 – exploring the motivational background for pushing for the empty chamber

Prior to initiating study 2, ferrets were allowed to acclimatize to the new set-up for 7 days. Similarly, an acclimatization period of 7 days was implemented between testing of the different set-ups. These set-ups were designed to assess whether the empty chamber had a functional value (exploring, patrolling, defecating; study 2a) and whether the door design had reinforcing values (pushing the door, tunnel around the door; study 2b).

2.8.1. Study 2a – testing the functional value of the empty chamber

The ferrets ($N = 3$ for each set-up) were randomly tested in three alternatives to set-up A_0 (A_1, A_2 and A_3) to assess how the changes to the design would influence MPP_{empty} (Fig. 2). Set-up A_1 comprised an extra compartment compared to set-up A_0. This extra compartment allowed evaluation of the ferret's motivation to push for the empty compartment to access a remote area to defecate and urinate (i.e. away from their sleeping box). Set-up A_2 comprised a see-through divider between EC and HC compared to the wooden divider in study A_0 to evaluate whether ferrets valued the opportunity to visually inspect EC. Set-up A_3 comprised a mesh tunnel around the perimeter of EC that could be freely accessed. This tunnel allowed the ferrets to freely perform territorial patrolling around the perimeter of EC, which is indicated as an important species-typical behaviour for ferrets (Moors and Lavers, 1981; Powell, 1979).

2.8.2. Study 2b – identifying potential reinforcing values of elements of the door design

To evaluate whether the door in itself had an intrinsic reinforcing value for the ferrets, resulting in them pushing for the empty compartment, MPP_{empty} was tested in a set-up where the ferrets ($N = 6$) were given a choice between accessing the empty compartment through the weighted door or freely accessing this compartment through a hole in the partition, which was realized by removing the cat flap (design B_0). Subsequently, MPP_{empty} was tested in three alternative set-ups to identify whether and which features of the door design may have influenced the ferrets' motivation to push the weighted door (design B_1–B_3, $N = 3$; Fig. 3). In set-up B_1 the (non-manipulable) nest box in HC was replaced by a manipulable sleeping bucket. Both the nest box and the sleeping box served the function of a secluded resting area, but the bucket could serve more functions as the ferret was able to play with it. In set-up B_2 the cat flap could swing both ways, thereby allowing the ferrets to visit EC and play with the cat flap without having to push the weighted door. Set-up B_3 had a small tunnel placed around the cat flap that could swing both ways to test whether the tunnel-like design of the weighted door affected its use.

2.9. Measurements

MPP_{food} and MPP_{empty} in study 1 were evaluated for each individual ferret and recorded in absolute weight (g) and in percentage relative to the ferret's bodyweight. MPP_{empty} was furthermore recorded as a percentage relative to MPP_{food}. Similarly, MPP_{empty} was evaluated separately for each ferret for each of the different set-ups in study 2. Similar to study 1, these values were recorded both in absolute value (g) as well as expressed in relative value (%) compared to MPP_{food} as determined in study 1. Behaviour of the ferrets was continuously recorded using infra-red surveillance cameras. Using these videos, the number, mean and total duration of visits to EC were analyzed.

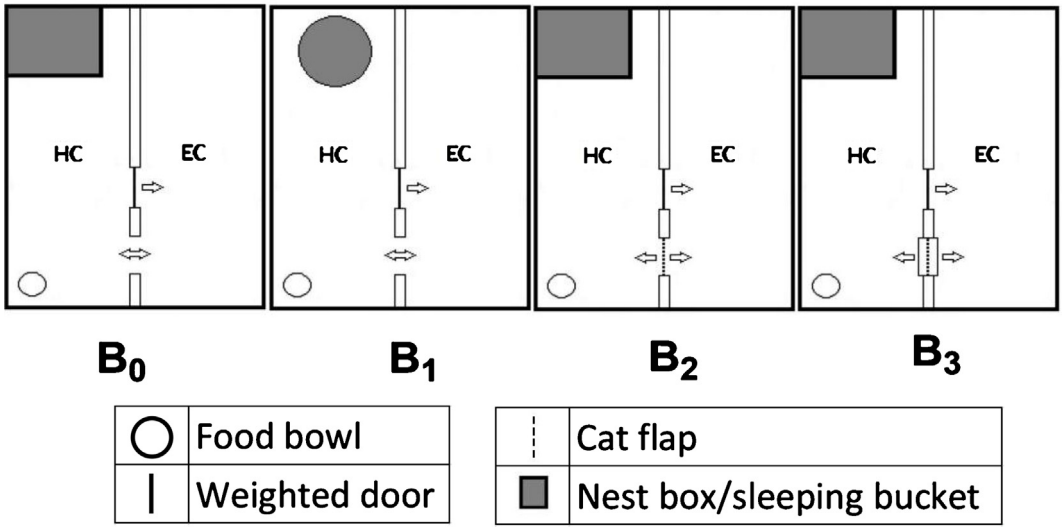

Fig. 3. The four set-ups that were used in study 2b. In these set-ups ferrets were given a free choice to gain access to EC (i.e. cat flap was removed and/or could be opened in two directions). Standard set-up without cat flap to allow free access to EC (B_0); set-up similar to B_0 but including a manipulable bucket instead of a nest box (B_1); set-up similar to B_0 but with a 2-way cat flap (B_2) and set-up similar to B_2 but with an extra tunnel around the cat flap (B_3).

2.10. Statistical analysis

Analyses were performed using IBM SPSS software (version 22.0). Data were expressed as mean ± SD; the probability level accepted for statistical significance was $p < 0.05$ unless stated otherwise. Normality of distribution of the residuals was determined with a Kolmogorov–Smirnov test and homogeneity of variances was analyzed with a Levene's test for equality of variances.

Differences between MPP_{food} and MPP_{empty} and changes in visit number and duration for food and an empty compartment in study 1 were analyzed using a repeated measures ANOVA. Initial visit number and duration for food and an empty chamber were compared using a paired *T*-test. MPP_{empty} in the different set-ups of study 2a (A_1, A_2, A_3) were compared to MPP_{empty} from study 1 (set-up A_0). Results were analyzed using a repeated measures ANOVA. MPP_{empty} in set-up A_0 and B_0 and MPP_{empty} as identified in set-up B_0 was compared to set-up B_1, B_2 and B_3 using descriptive statistics due to a large number of missing values and the small sample size ($N = 3$).

3. Results

3.1. Study 1 – suitability of the design

MPP_{food} was 1325 ± 213 g (950–1575 g; $N = 12$), which equalled 143 ± 31% (101–200%) of the ferrets' bodyweight. Ferrets did attempt to push the weighted door above MPP_{food}, but were unable to do so. MPP_{empty} was 1169 ± 193 g (850–1425 g; Fig. 4). Although a statistically significant difference was present between MPP_{food} and MPP_{empty} ($p = 0.024$, $F = 6.818$), this difference was very small: ferrets pushed 89 ± 13% (60–100%) of MPP_{food} for the empty chamber.

When the doors were unweighted, ferrets visited EC 32 ± 18 times per day for 5 ± 6 min each time to gain access to food, compared to 16 ± 9 times per day for 2 ± 1 min each time when EC was empty ($p = 0.019$ for visit number and $p = 0.095$ for visit duration). The number of visits to both the empty chamber and the chamber with food decreased with increasing weights on the door ($p < 0.001$ in both situations). The number of visits to EC remained higher when food was present than when EC was empty ($p = 0.001$; Fig. 5a). In addition, the ferrets paid longer visits to EC with increasing weights when food was present in this chamber ($p = 0.043$), whereas visits to EC shortened when EC was empty ($p = 0.018$; Fig. 5b). Total daily visit duration remained constant when food was placed in EC ($p = 0.192$) whereas total visit duration decreased when EC was empty ($p = 0.000$; Fig. 5c).

3.2. Study 2a – testing the functional value of the empty chamber

Ferrets pushed 70 ± 15% of MPP_{food} (60–87%; $N = 6$) for the empty chamber in the design with the extra chamber (A_1) versus 75 ± 11% (52–74%) in the design with a see-through divider (A_2) and 66 ± 12% (69–87%) in the design with the mesh tunnel (A_3). None of these values were statistically different from the standard design from study 1 (A_0: 89 ± 13%) ($p_{A_0-A_1} = 0.267$; $p_{A_0-A_2} = 0.297$; $p_{A_0-A_3} = 0.071$;Fig. 6a).

3.3. Study 2b – identifying potential reinforcing values of elements of the door design

MPP_{empty} was lower when the ferrets did not have to push the weighted door to reach EC (B_0: 53 ± 22%) compared to the situation in which they were required to work to gain access to EC (A_0: 89 ± 13%; Fig. 6b). In the three alternative set-ups, the ferrets pushed less than in set-up B_0 (26 ± 14% (B_1), 36 ± 8% (B_2) and

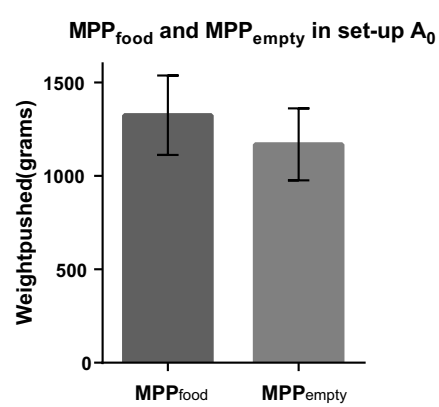

Fig. 4. Maximum price paid for food (MPP_{food}) and the empty chamber (MPP_{empty}) by the ferrets in study 1, set-up A_0 ($N = 12$).

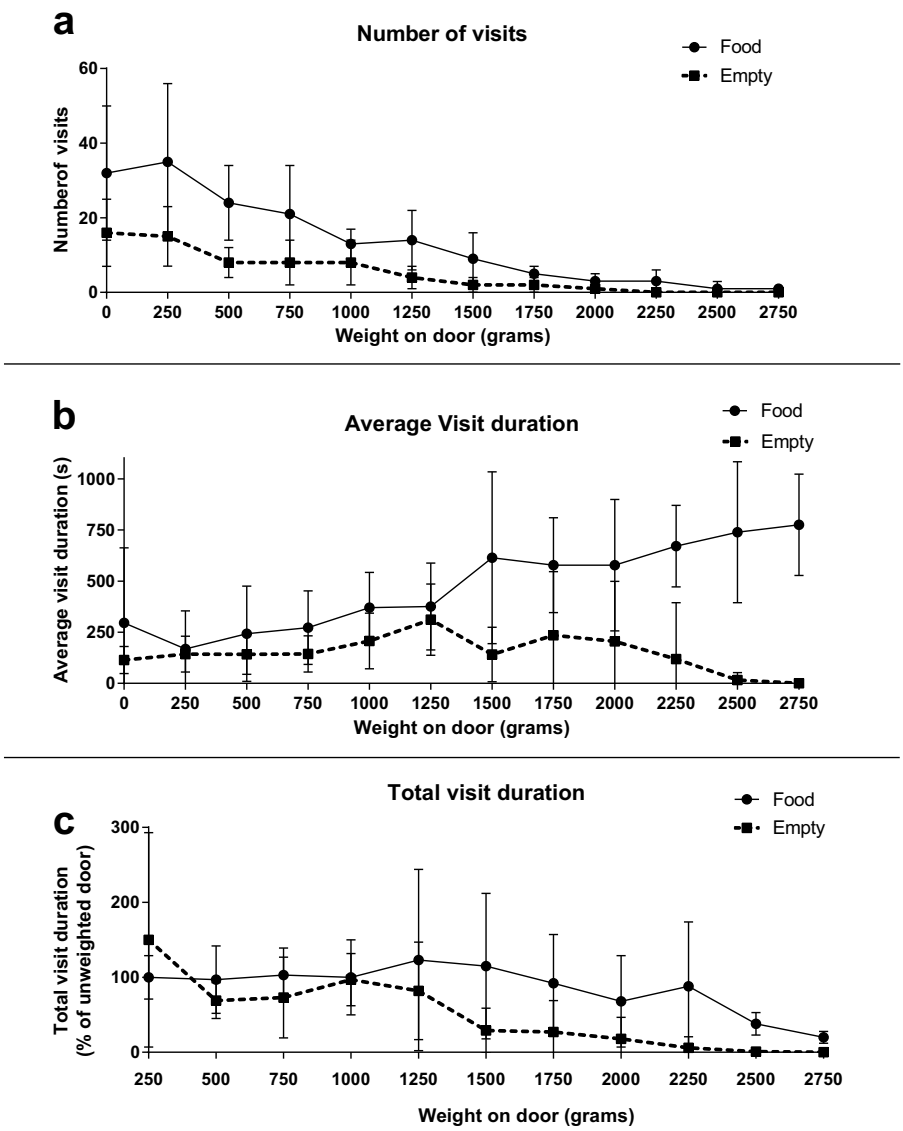

Fig. 5. Number of visits (a), average visit duration (b) and total visit duration (c) of ferrets to EC (containing food; solid line, and an empty room; dashed line), tested in set-up A_0 ($N = 12$).

37 ± 21% (B_3) of MPP_{food}). Set-up B_1 (in which a manipulable sleeping bucket was provided) resulted in the lowest MPP_{empty} (Fig. 6c).

4. Discussion

In this study, a two-chamber closed economy consumer demand set-up using a weighted door was tested for its suitability to determine the ferrets' motivation for specific resources by evaluating whether it fulfilled the following three prerequisites: (1) MPP_{food} should reflect MPC; (2) the task should be perceived as strenuous, as indicated by a decrease in number of visits and an increase in the duration of visits upon increasing the effort to gain access to EC and (3) MPP_{empty} should be low and sufficiently distinctive from MPP_{food} to enable detecting differences in MPP between the different resources presented in EC.

The first prerequisite was most likely met, as the ferrets attempted to push the door above MPP_{food}, but were unable to do so. MPP_{food} of the ferrets (143 ± 31% of bodyweight) was similar to the MPC of mink (147 ± 43% of bodyweight) (Cooper and Mason, 2001) and both Silver foxes (Hovland et al., 2006) and rabbits (Seaman et al., 2008) have shown to pay the highest price for food. Therefore, it is considered likely that the MPP_{food} found in this study reflects the true maximum push capacity of these ferrets, thereby enabling this value to be used as a benchmark for comparison of other resources and establishing their value.

The second prerequisite was also met, as the number of visits declined and the duration of visits to EC increased with increasing effort to gain access to food. A similar reorganization of behaviour has been observed in other consumer demand studies (Cooper, 2004; Sherwin and Nicol, 1996). Based on these results, a weighted door seems a suitable task to use in a consumer demand study for ferrets.

In contrast to the first two prerequisites, the third prerequisite was not met during this study, as the ferrets were found to push almost 90% of their maximum push capacity (MPP_{food}) to gain access to an empty chamber. This is considerably higher than results found in other animal species. Mink, for example, were found to push 67% of their MPC (which was determined as the MPP for a water pool) for an empty chamber (Mason et al., 2001).

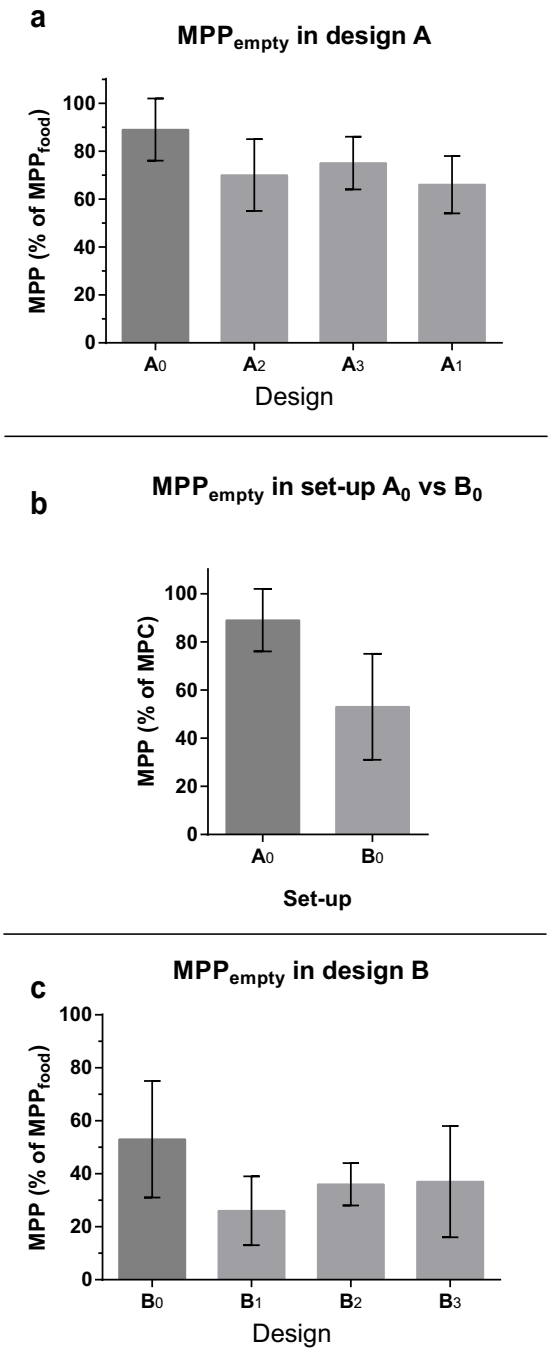

Fig. 6. Bar chart demonstrating the ferrets' MPP_{empty} for design A_0–A_4 (a), for design A_0 versus B_0 (b) and design B_0–B_3 (c). A_0 = standard set-up (N = 12), A_1 = standard with an extra chamber (N = 3), A_2 = standard with a see-through divider (N = 3), A_3 = standard with a mesh tunnel around the perimeter (N = 3), B_0 = standard without a cat flap (free access to EC) (N = 6), B_1 = design B_0 with a manipulable sleeping bucket instead of a nest box (N = 6), B_2 = design B_0 including a 2-way cat flap, B_3 = design B_2 with a tunnel surrounding the 2-way cat flap (N = 3).

Although the difference between MPP_{empty} and MPP_{food} was found to be statistically significant, the relative difference between the two was deemed too small to be able to assess and distinguish between the values of different resources. As a result, the third prerequisite was deemed not to have been met with the set-up used in this study.

To examine whether the third prerequisite could be met by adapting the design and to assess why the ferrets in our study pushed almost as hard for food as for an empty chamber, study 2 was performed during which we tested whether and which aspects of the design (e.g. functionality of the empty chamber (set-up A_1–A_3) or reinforcing value of elements of the door (set-up B_0–B_3)) could have resulted in the relative high MPP_{empty}.

None of the three set-ups of design *A* (with extra compartment, a see-through divider or a mesh tunnel) yielded a significantly lower MPP_{empty} compared to study 1. In other words, the hypothesized motivational backgrounds for pushing for access to the empty chamber could not be confirmed and we were not able to adapt the design in such a way that the functional value of EC was significantly decreased.

Comparison between set-up A_0 and B_0 (in which ferrets were allowed a choice between free access or pushing the weighted door to gain access to EC) showed that ferrets pushed less when they could freely access EC through a hole in the partition. MPP_{empty} decreased to $53 \pm 22\%$ of MPC, which is comparable to that of mink (67%, Mason et al., 2001). This indicates that the empty room does have a value for the ferrets. Additionally, one or more elements of the door design may also have intrinsic reinforcing value for the ferrets, as they remained motivated to some extent to push the weighted door. Therefore, another study was performed to test the hypothesized effects of reinforcing elements of the weighted door on MPP_{empty} (e.g. the tunnel around the door, manipulating the door/cat flap).

In all of the set-ups of design B, the ferrets used the weighted door regularly. A possible explanation for this seemingly unnecessary pushing behaviour could be that ferrets need a high level of stimulation and that, even though it was actually designed as a task, the weighted door evokes object manipulation in a stimulus poor environment. Support for this explanation comes from the observation that pet ferrets show high levels of exploration and are focused on tactile stimulation (Fisher, 2006) and ferrets in barren cages were found to be distressed, showing signs of stereotypic behaviour (e.g. bar chewing and head swaying) and/or becoming lethargic (Cruden, 2011).

The small difference in MPP_{empty} when allowed free access to EC in set-up B_2 and B_3 indicates that neither the action of pushing the door nor the tunnel around the weighted door could account for the attractiveness of the door. The ability to manipulate the sleeping bucket in HC (set-up B_1) lowered MPP_{empty} the most. Thus, the ability to manipulate an object may be an attractive element of the door and the ferrets apparently valued the ability to manipulate a mounted door or cat flap lower than the ability to play with a manipulable item such as the plastic bucket. Pet ferrets are often found dragging their toys to secluded locations (Fisher, 2006). It is possible that moving the sleeping bucket (which could be moved) approximates this species-typical behaviour better than the ability to play with the mounted door or cat flap (which cannot be dragged around), thereby explaining the ferret's overall higher motivation to play with the bucket.

Although results from study 2 provide some insight into the underlying motivation for the ferrets to gain access to the empty compartment and use the door, results of this study did not reveal a solution to ensure that the third prerequisite would be met without compromising the set-up of the consumer demand study. Thus, alternative methods should be considered in order to reliably establish the value of resources for ferrets.

One option to overcome the issue of the high MPP_{empty} would be to use an alternative index for determining the value of the resources. For example, the price elasticity of demand index uses the rate of decline in consumption per unit increase in cost (Houston, 1997). This index makes it possible to distinguish resources for which the number and duration of visits remain relatively constant with increasing prices (such as food) from resources for which the number and duration of visits decline more rapidly

(such as an empty chamber). Price elasticity of demand, however, has several disadvantages including (a) the possibility for a resource to have more than one elasticity value (Dawkins, 1983; Houston, 1997); (b) overestimation of the value for resources that quickly lead to satiation, as these are associated with low price elasticity (Kirkden et al., 2003; Kirkden and Pajor, 2006); (c) underestimation of the value of resources that are consumed in great amounts in the initial phases (Kirkden et al., 2003; Kirkden and Pajor, 2006; Seaman et al., 2008; Warburton and Mason, 2003); (d) difficulties to detect elasticity of demand in an experiment as the demand can be relatively equal over a large price range (Kirkden et al., 2003); (e) difficulties to determine the correct size of the price unit rise, as it is essential that each unit rise in price is regarded as equal by the animal (Cooper, 2004); and (f) the necessity to keep the reward size constant, which might devalue all-or-none goods (Mason et al., 1998). Alternative to the maximum price paid and price elasticity of demand index, the consumer surplus index can be used. This index measures the area under the demand curve (Mason et al., 2001; Seaman et al., 2008). Although this index is deemed as more valid than the price elasticity of demand index due to its omission of disadvantages (a)–(c), it does use the same curve as the price elasticity of demand index, thereby sharing disadvantages (d)–(f) (Houston, 1997; Kirkden et al., 2003). These disadvantages render both indices unsuitable for our goal and are therefore not considered a viable solution.

The second option would be to use a set-up with more than two chambers. Although such set-ups have the disadvantage that they require the animals to divide their time and energy between multiple resources (thereby potentially yielding a lower MPP for less preferred resources), such a set-up may provide the ferrets with a larger choice in activities thereby potentially lowering the ferret's motivation to push the weighted door for the empty chamber. Thus, a three- or multi-chamber set-up (e.g. Hovland et al., 2006; Mason et al., 2001; Seaman et al., 2008) may be suitable to overcome the issues regarding the high motivation to push for the empty door, thereby allowing us to test the ferrets' motivation for resources and rank these according to their value. Further research is, however, necessary to determine whether this indeed is a feasible and suitable alternative to test the value of resources for ferrets.

5. Conclusion

The current study shows that the closed-economy two-chamber set-up is not suitable for testing the ferrets' motivation for different resources as MPP_{empty} and MPP_{food} were relatively similar, thereby leaving little room for distinction between the value of different resources. The ferrets showed high motivation to push a weighted door to gain access to an empty room, even when they could freely access this room through a two-way cat flap or a hole. In the latter situation, motivation to push the weighted door did decrease, however, indicating that motivation to push for the empty room cannot solely be attributed to reinforcing properties of the door design, but most likely also to functional aspects of the empty room. It appears most likely that the ferrets' high MPP_{empty} originates from a high desire for (tactile) exploration, which renders this an important factor to consider when designing a consumer demand study for ferrets. To determine the value of enrichments for ferrets, other set-ups, such as a three- or multi-chamber set-up, should be considered.

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