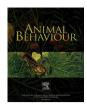
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Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Are all motivation tests the same? The effect of two adaptations to a three-chamber consumer demand study in ferrets



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ARTICLE INFO

Article history:
Received 27 March 2017
Initial acceptance 10 May 2017
Final acceptance 26 September 2017
Available online 1 December 2017
MS number 17-00277R

Keywords: consumer demand study enrichment ferret maximum price paid motivation Ferrets, Mustela putorius furo, are increasingly used in infectious disease studies, particularly in influenza research. Which specific housing conditions and environmental enrichments are of particular importance for ferrets have not been part of a systematic evaluation. The motivation ferrets showed to reach different enrichments was assessed in multiple consumer demand study set-ups. To address the question whether these consumer demand set-ups give similar results, we assessed the effects of two ways of offering enrichments concurrently instead of consecutively. Six ovariectomized female ferrets were successively tested in a seven-chamber (7Ch), three-chamber (3Ch) and three-chamber 'all-butone' (ABO) set-up. We compared the maximum price paid, visit number, visit duration and interaction time with the enrichments in the 3Ch versus the 7Ch and ABO set-ups, respectively. Compared to the 3Ch set-up, the ferrets in the ABO and 7Ch set-up showed a lower motivation to access, paid fewer and shorter visits to and interacted less with the enrichments. In the 7Ch, the ferrets especially showed a lower motivation for the less preferred enrichments and the empty chamber. These findings indicate that testing all the enrichments concurrently in the 7Ch set-up forced the ferrets to make more economic decisions, thereby providing more valuable information on how different enrichments are valued relative to one other. Adding preferred enrichment items to the home chamber, as was done in the ABO set-up, might have reduced the motivation to access or look for additional enrichment items. However, this set-up might not have a closed economy, making the ABO set-up unsuitable. Based on these findings, we advise testing all the enrichment categories concurrently instead of consecutively and keeping the number of items in the home cage to a minimum when performing a consumer demand study, as this appears the most optimal set-up to determine motivational priorities for resources in ferrets.

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Consumer demand studies are commonly used and regarded as a valid method to assess an animal's motivation for different types of environmental enrichment. This technique has been derived from human micro-economics and has been proposed as a tool to identify behavioural needs (Dawkins, 1983) as it can aid in understanding what animals 'want' (i.e. are motivated to access, Berridge & Robinson, 2003). A consumer demand study uses an operant conditioning task in which the 'price' (e.g. number of responses) to

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gain access to a resource is increased or the available 'income' (e.g. available time to respond) is decreased (Cooper & Mason, 2001; Dawkins, 1990). Ultimately, the 'price' an animal is willing to pay for access to an enrichment indicates the motivation an animal has to reach it, and how important it is for that animal to have access to that specific enrichment (Kirkden & Pajor, 2006). Consumer demand studies are therefore often used to substantiate which changes to an animal's housing should be made to improve their welfare (e.g. Mason, Cooper, & Clarebrough, 2001; Seaman, Waran, Mason, & D'Eath, 2008).

Reijgwart et al. (2015) designed a two-chamber consumer demand study to identify enrichments that could be provided to ferrets, *Mustela putorius furo*, to refine studies using these animals.

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This set-up proved to be unsuitable to test ferrets, however, as they would push to their maximum ability to reach an empty chamber. This study further indicated that the items in the home chamber influenced the ferrets' motivation to enter an empty chamber. The subsequent search for a suitable consumer demand set-up for ferrets resulted in two possible alternative set-ups: a three-chamber and a multichamber set-up (e.g. Hovland, Mason, Bøe, Steinheim, & Bakken, 2006; Mason et al., 2001; Seaman et al., 2008). It was not clear, however, whether these set-ups would give similar results when applied to ferrets.

In the literature, there are many issues regarding how a consumer demand study can optimally be designed and interpreted. First, an animal should be tested in a closed economy (i.e. only providing access to the enrichment during the experiment), as testing in an open economy (i.e. giving the animals access to the enrichments outside the test environment) might lower the motivation for enrichments in the study (Ladewig, Sørensen, Nielsen, & Matthews, 2002; Mason, McFarland, & Garner, 1998). Second, a naturalistic operant task (such as a push door or a narrow gap) should be used, as it requires little training and is least prone to operant-reinforcer bias (Cooper, 2004; Kirkden, Edwards, & Broom, 2003; Mason et al., 1998). Third, the maximum price paid (MPP) or reservation price index, the price at which the animal is no longer willing to perform the task, should be used to calculate the animal's motivation as it is considered the most appropriate for the assessment of unsubstitutable, discrete and indivisible resources such as enrichments (Cooper, 2004; Cooper & Mason, 2001; Jensen & Pedersen, 2008; Mason et al., 1998). Fourth, to be able to interpret the price the animals pay for resources correctly, it is vital to determine the negative control (i.e. the minimum price the animal will pay) and positive control (i.e. the maximum price the animal is able to pay; Dawkins, 1983). As a negative control, the animal's motivation for an empty chamber is often measured in order to quantify how motivated the animal is to reach additional space and/or to perform the task itself. As a positive control, the animal's maximum push capacity (MPC), that is, the maximum effort that the animal is able to exert to accomplish the task, is established. This parameter can be used as a yardstick to relate the findings to. The animal's motivation for food or water is often used as the MPC as these are essential needs, for which the animal will presumably perform to its maximum ability (Dawkins, 1983; Matthews & Ladewig, 1994). These minimum and maximum motivation levels can subsequently be used to determine where on the motivational scale the values of different enrichments lie.

To our knowledge, whether offering enrichments concurrently or consecutively affects the results obtained in consumer demand studies has not been studied. Therefore, we compared the results of a three-chamber (3Ch) consumer demand set-up with a sevenchamber (7Ch) set-up (comparison 1). Additionally, we compared the results of the 3Ch set-up with the results of a three-chamber 'all-but-one' (ABO) set-up (comparison 2) to assess the effect of adding freely available enrichment items to the home chamber. In the 7Ch set-up, the ferrets are expected to make more economic choices than in the 3Ch set-up, in view of the limited time (and energy) available to work for and visit the concurrently provided enrichment items. In the ABO set-up, the ferrets are expected to be less motivated to access additional enrichment items than in the 3Ch set-up, as there are highly valued items freely available in the home chamber already fulfilling some motivations. We therefore predicted that offering the enrichments concurrently in the 7Ch set-up and adding enrichment items to the home chamber in the ABO set-up would result in a lower MPP, visit number, visit duration and interaction time with the enrichments than in the 3Ch set-up.

METHODS

Ethical Note

This study was ethically approved by the Animal Care and Use Committee of the Institute for Translational Vaccinology (Intravacc, DEC 201400137). As this was a study into the enrichment priorities of ferrets, there were few welfare implications. The ferrets were housed alone when they were being tested, which might have caused some distress. However, it is not yet determined whether ferrets are a truly social species (i.e. whether they suffer when housed alone). In the 7Ch set-up, the ferrets could always push a door to gain access to conspecifics.

Animals, Housing and Husbandry

For the study, six female surgically neutered (ovariectomized) ferrets were used that were obtained from Schimmel B.V. (Scherpenzeel, Netherlands), weighed $1035 \pm 131 \, \mathrm{g}$ and were approximately 1 year old at the start of the experiment. The ferrets were ovariectomized to prevent the onset of oestrus, which could affect their behaviour and might lead to anaemia, weight loss, alopecia and even bone marrow depression if the animal is not bred (Fox, Bell, & Broome, 2014). The ferrets were housed under the conditions described in Reijgwart et al. (2016), namely indoors, between 19 °C and 23 °C, on an 8:16 h light:dark schedule with auditory stimulation. They were group housed between experiments in floor pens (163x94 cm) with sawdust, a flexible plastic bucket and ad libitum water (from a nipple) and food (ferret balance pellets in a stoneware bowl; Hope Farms, Woerden, Netherlands). The ferrets' health and overall condition were monitored prior to and throughout the study.

Enrichments

Enrichments from six different enrichment categories were tested: sleeping enrichment, water enrichment, foraging enrichment, social enrichment, tunnels and balls; Table 1).

These enrichment categories were chosen to accommodate behaviours seen in feral ferrets, where each category represents a different behavioural motivation (see Reijgwart et al., 2016). For each enrichment category two or three items with different characteristics were offered in one enrichment chamber to increase the chance of testing the motivation for the preferred item within the category. These items were chosen based on variability within a category and practicality in a laboratory setting. Additionally, an empty chamber was tested to control for the value of extra space, patrolling and the rewarding properties of the task itself (i.e. negative control). Food was used as a resource to serve as a positive control, that is, to determine the MPC of the ferrets (see Reijgwart et al., 2015).

Experimental Housing

During the experiment, the ferrets were subsequently individually housed in three types of closed-economy consumer demand set-ups, each consisting of one home chamber, an empty control chamber and either one or six enrichment chambers for the 3Ch or 7CH set-up, respectively.

Apparatus

Between the chambers there was a 70 cm high, 6 mm thick phenolic-faced plywood divider. The divider was equipped with a mesh window through which the ferrets could see whether and which items were present in the chamber. This was done to ensure that the ferrets were always aware of the items present in each

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