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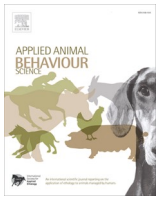

Elastic motivation for circuit running behaviour in captive African striped mice *Rhabdomys dilectus*: A consumer demand approach

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ABSTRACT

Captive environments often result in repetitive locomotor behaviours in animals, yet the motivation for these behaviours remains poorly understood. We investigated whether circuit running in African striped mice *Rhabdomys dilectus* represents a necessary coping mechanism or a flexible, cost-sensitive behaviour, which we tested using a consumer demand framework. Twenty mice displaying circuit running were individually housed in cages that limited this behaviour. Mice accessed a test chamber by travelling through a short (low-cost, Lc) or long (high-cost, Hc) connecting pipe, with the incentive value manipulated to create either a large (high, Hi) or small (low, Li) space, creating four treatments: LcHi, LcLi, HcHi, and HcLi. Mice displayed a higher proportion of circuit running in treatments with greater incentives (LcHi, HcHi) compared to those with restricted space (LcLi, HcLi), and the duration spent in the test chamber followed a graded pattern (LcHi > LcLi > HcHi > HcLi). Demand was classified as elastic or inelastic based on changes in behaviour relative to cost. Circuit running decreased as costs increased, indicating an elastic demand. Our findings indicate that circuit running in *R. dilectus* is flexible rather than fixed, challenging the interpretations of repetitive behaviour as an inflexible coping response. Our study also demonstrates the value of economic models for assessing behavioural motivation in captivity and suggest that repetitive locomotor behaviours may serve adaptive, facultative functions under constrained conditions.

1. Introduction

Captive animals frequently develop repetitive, highly structured behaviours that are usually referred to as stereotypical behaviours. These are typically defined as repetitive, invariant patterns without apparent function or goal, and are widely considered as potential indicators of poor welfare in restrictive environments (Mason, 1991; Mason et al., 2007; Latham and Mason, 2004). However, not all repetitive behaviours necessarily indicate dysfunction or poor welfare, and some may represent flexible behavioural strategies in response to altered environmental contingencies (Latham and Mason, 2004). Understanding the mechanisms behind the development and expression of repetitive behaviours can help us understand why it arises and whether we need to prevent its occurrence.

One widely discussed explanation for the persistence of stereotypical behaviour is the "coping hypothesis", which proposes that these behaviours function to alleviate stress or frustration, thereby serving a functional role under captive conditions (Rushen, 1993; Wechsler, 1995). There is some support for this hypothesis; for example, performance of locomotory stereotypical behaviour in bank voles *Clethrionomys glareolus* has been associated with reduced physiological signs of stress (Cooper and Nicol, 1993). However, empirical support is mixed, and distinguishing whether a behaviour functions as a necessary coping mechanism or arises from other motivational processes remains challenging. Some stereotypical behaviours are apparently resistant to environmental change due to underlying neural alterations (Mason and Latham, 2004; McBride and Hemmings, 2009), while others may persist because they are inherently rewarding or because opportunities for displaying natural behaviours are limited (Mason and Latham, 2004; Würbel, 2006).

Understanding the motivational basis of repetitive behaviours is important for interpreting their function and welfare implications. One promising approach is the application of economic demand theory (Dawkins, 1983; Mason et al., 1998), originally developed in human behavioural economics (McConnel and Brue, 2005). In this framework, animals are required to "pay" increasing costs to access a resource or to perform a behaviour, enabling us to assess how strongly motivated they are to obtain the resource. If motivation is strong (inelastic demand), the

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behavioural response is rigid and even maintained when the cost increases significantly. This suggests that the behaviour is highly motivated or essential, analogous to a "necessity" in economic terms. However, if motivation is weak or flexible (elastic demand), the behavioural response is flexible, and it declines as the cost to perform it increases. This indicates that the behaviour is non-essential or optional under constrained conditions-comparable to a "luxury" in economic terms (Vinke et al., 2008). This method has been applied to assess the value of resources and behaviours in several species (Cooper and Mason, 2000; Würbel, 2006). For example, Cooper and Mason (2000) showed that American mink *Mustela vison* was willing to pay varying costs to access resources such as hay, water baths and toys, demonstrating differing levels of motivation.

In this study, we investigated the motivational basis of repetitive locomotor behaviour, specifically circuit running, in captive African striped mice *Rhabdomys dilectus*. Circuit running has been identified as a common repetitive behaviour in this species under captive conditions and considered a stereotypy (Schwaibold and Pillay, 2001; Jones et al., 2008), although its functional significance remains unclear. Rather than assuming that circuit running necessarily reflects a stereotypy associated with coping, we aimed to assess the flexibility of this behaviour in response to environmental costs.

Using a consumer demand design, we manipulated the energetic cost required by striped mice to travel through pipes of varying lengths to access space (an incentive) to perform circuit-running behaviour. We tested whether circuit running in striped mice is a necessity (inelastic demand) or a luxury (elastic demand). If circuit running serves as a coping mechanism, we predicted that mice would pay high costs to perform this behaviour, consistent with inelastic demand. Alternatively, if circuit running is a flexible behaviour, demand should be elastic, decreasing as costs increase. This approach parallels human consumer behaviour, in which the demand for essential goods (e.g. bread) is typically inelastic, while the demand for luxury items (e.g. cars) is elastic, declining with increasing cost (Vinke et al., 2008).

2. Materials and methods

2.1. Model species

The African striped mouse *Rhabdomys dilectus* is a small (40–80 g), diurnal murid rodent distributed widely across the mesic regions of southern Africa (Skinner and Chimimba, 2005). Under captive conditions, a large proportion of individuals spontaneously develop repetitive locomotor behaviours, mainly circuit running, which exhibits strong heritability (Schwaibold and Pillay, 2001; Jones et al., 2008). Circuit running is characterised by repetitive, structured movement along a fixed path within the enclosure (Jones et al., 2008). Given its consistent occurrence within individuals, *R. dilectus* represents a useful model for studying the motivational basis of repetitive locomotor behaviour.

2.2. Husbandry

Test striped mice used in this study were bred from a colony housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14 L:10D, lights on at 05:00 h; 22°C–24°C; 30–60 % relative humidity). Prior to experiments, all mice were individually housed in Lab-o-tec cages™ (L × H × W: 425 mm × 150 mm × 240 mm). Solitary housing does not induce stress in *R. dilectus* (Mackay et al., 2014) and reflects their natural solitary social system (Schradin and Pillay, 2005).

Cages contained ~ 3 cm wood shavings as bedding and a handful of *Eragrostis* sp. grass and ~ 5 g of paper tissue as nesting material, a small twig for enrichment and a PVC nest-box (L × H × W: 130 mm × 90 mm × 100 mm, open at both ends). To become familiar with the test apparatus (see below), subjects were provided with a short piece of pool pipe (± 150 mm length, 41 mm diameter), which also served as enrichment. Epol™ mouse cubes (Epol, Pretoria West, South Africa) and water were provided ad libitum, and supplemented with approximately 5 g fruit/vegetables and approximately 5 g of parrot seed mix every second day. Cages were cleaned weekly and the bedding and nesting material replaced.

2.3. Subject selection

We screened 81 adult striped mice (>60 days of age) for circuit running behaviour by video-recording each individual for five consecutive days for 30 min daily between 09h00 and 12h00 (their peak activity period; Pillay, 2000); no human observers were present during video-recordings. Circuit running was defined as repetitive movement along a fixed path (circular or figure-eight patterns) with at least three consecutive returns to a common point per bout. Only individuals consistently exhibiting circuit running (n = 20; 10 males, 10 females) were included in the experiment. Striped mice not expressing circuit running were excluded, because the focus of the study was on the flexibility of an already established repetitive behaviour under variable environmental costs.

2.4. Experimental design

The experimental set up involved a home cage (L × H × W: 230 mm × 175 mm × 150 mm) that was connected to a test chamber (L × H × W: 460 mm × 350 mm × 300 mm), using plastic pool pipes of two lengths, either 1 m (short) or 3 m (long), both with a diameter of 41 mm (Fig. 1). The home cage had food, water, wood shavings and nesting material (as described above) and several enrichment devices, whereas the test chamber contained only wood shavings. For the experiments, the test chamber was utilised intact or halved in size with a divider (L × H × W: 265 mm × 150 mm × 205 mm; Fig. 1).

Striped mice require a large space for circuit running, which was restricted in the home cage. Therefore, the intact test chamber was a high value incentive, and the halved test chamber was low value. Consequently, test subjects had to pay a cost of travelling through pipes of different lengths to reach a low and high value resource, resulting in four treatments: 1) short pipe (1 m) - large test chamber (Low-cost/High-incentive, designated LcHi); 2) short pipe (1 m) – reduced test chamber size (Low-cost/Low-incentive, designated LcLi); 3) long pipe (3 m) – large test chamber (High-cost/High-incentive, designated HcHi); and 4) long pipe (3 m) – reduced test chamber (High-cost/Low-incentive, designated HcLi).

Prior to being exposed to the treatments, the striped mice were habituated to the setup of a large test chamber (high incentive) being attached to their home cage with a 1 m pipe for 3–5 days. A piece of fruit was added to the test chamber to attract the mouse across. Thereafter, each striped mouse was exposed to the treatments in random sequence. They spent two days in each treatment, equating to eight consecutive days in experiments. The activity (behaviour) of the subjects in the test chamber and home cage was video-recorded from 09h00 to 12h00. No human observers were present in the room during recordings. When all treatments were completed, the mice were returned to the colony and maintained as described above.

From video footage, we recorded the total duration (in seconds) that mice spent in the test chamber. In addition, the duration of the following behaviours was recorded: circuit running (defined above), digging (digging in the wood shavings), exploring (walking/running around the tank in a non-stereotypic manner), inactive (standing/still for more than 3 seconds, resting), grooming (scratching and licking), and other (other behaviours of low occurrence). The duration of behaviours in the test chamber were converted to a proportion of the total time a striped mouse spent in the test chamber.

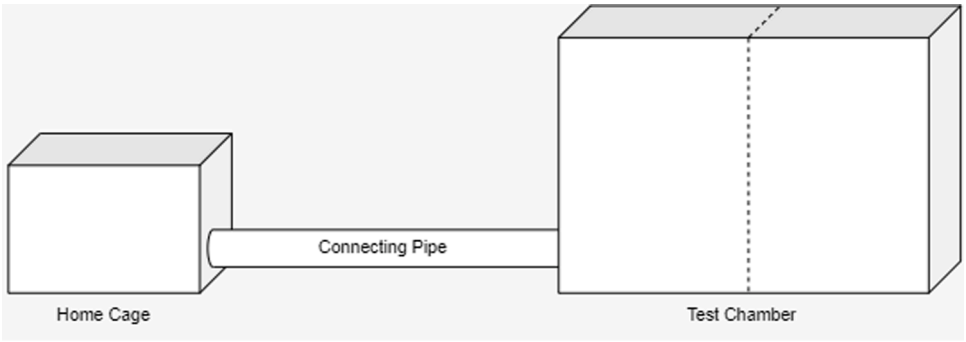

Fig. 1. Illustration of the experimental set up. The home cage was connected to the test chamber with a pipe of either 1 m or 3 m (low cost or high cost, respectively) in length. The dotted line in the experimental tank indicates how the incentive was altered, being either low (half the tank) or high (full tank).

2.5. Data analysis

Statistical analyses were conducted using R software (version 4.4.2; www.R-project.org). Data distributions were assessed visually via Q-Q plots. The data were non-normally distributed (positively skewed), so non-parametric analyses were used. The duration spent in the test chamber were analysed using a Generalised Linear Mixed Model (GLMM) with a Tweedie distribution (log link). The models included treatment and sex as fixed factors. The proportion data (circuit running and other behaviours) and were calculated as a proportion of total duration and analysed using zero-inflated beta regression models (logit link). Individual identity was included as a random factor. In all analyses P values were generated using Type II Wald chi-squared tests. Significant predictors were analysed further using Tukey post hoc tests. All analyses were two-tailed and model significance was set at 0.05.

To visualise the relationship between the duration spent in and the frequency of visits to test chamber in the treatments, we used LOESS smoothing (locally weighted scatterplot smoothing) to fit descriptive trendlines to the data. LOESS is a non-parametric smoothing technique that fits local regressions to overlapping subsets of the data to reveal underlying patterns without assuming a specific functional form. To facilitate visual comparison and stabilise the smoothing, we scaled duration values to a mean of 0 and a standard deviation of 1, because of the different ranges in the values for these variables.

The demand elasticity (E_d) for stereotypical behaviour was determined using the economic equation:

$$E_d = \frac{(\Delta Q/\overline{Q})}{(\Delta P/\overline{P})} \quad (1)$$

Where Q is the quantity demanded and P is the price of the item under consideration. If the value of E_d (demand elasticity) is greater than 1, the demand is elastic and an E_d less than 1 indicates that the demand is inelastic (McConnel and Brue, 2005). In our study, Q represented the proportion of circuit running behaviour in the test chamber and P was the price to perform the behaviour. This price was determined by ranking the treatments in a 'cheapest' to 'most expensive' manner, with low-cost/high-incentive (LcHi) being the 'best value for money' (low effort, large incentive), increasing in price with low-cost/low-incentive (LcLi), high-cost/high-incentive (HcHi), and high-cost/low-incentive (HcLi) being the most expensive treatment because the effort is high for a minimal incentive. Numerical values were assigned to each treatment for the 'price' for P in Eq. 1, as follows: LcHi: $P = 1$; LcLi: $P = 2$ because the cost is the same as LcHi, but the incentive is only half, and thus it costs double the price; HcHi: $P = 3$ because it has the same incentive as LcHi but costs triple as much (i.e. 3 m pipe); and HcLi: $P = 6$ because the incentive is the same as LcLi but at triple the cost.

2.6. Ethics

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand, South Africa (AESC number 2009/6/2 A).

3. Results

Of the 20 striped mice used, only two individuals (10 % of all subjects) displayed circuit running in the home cage, which occurred in the high-cost treatments (i.e. long pipe). The others displayed circuit running in the test chamber or not at all.

3.1. Use of the test chamber

Treatment had a significant effect on the total duration that striped mice spent in the test chamber ($\chi^2 = 138.55$, df = 3, $p < 0.001$). There was a graded response by treatment, LcHi > LcLi > HcHi and HcLi (Tukey posthoc tests all $p < 0.001$; Fig. 2), indicating that the total duration was greater when the connecting pipe was shorter, and the test chamber was larger. Sex was not a significant predictor of total duration ($\chi^2 = 1.70$, df = 1, $p = 0.192$).

3.2. Relationship between frequency and duration of visits

Fig. 3 shows the relationship between the time spent and the number of visits to the test chamber. For the LcHi treatment, there is a positive relationship between duration and frequency; striped mice that visited the test chamber more often also spent longer durations per visit. The relationship was weaker and more variable in the LcLi, HcHi and HcLi

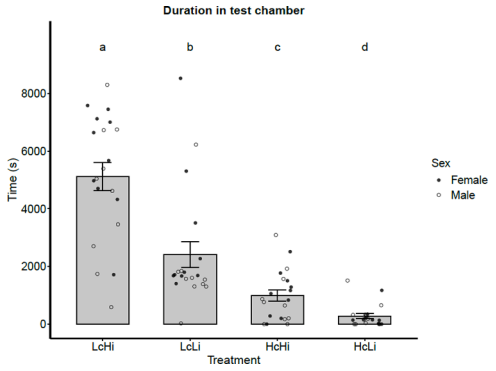

Fig. 2. Mean (± SE) total duration (s) spent in the test chamber in four treatments (LcHi, LcLi, HcHi, HcLi) in captive *Rhabdomys dilectus*. Individual data points are shown, with females shown as solid circles and males as open circles. Different letters above bars indicate statistically significant differences between treatments (Tukey post hoc comparisons, $p < 0.05$).

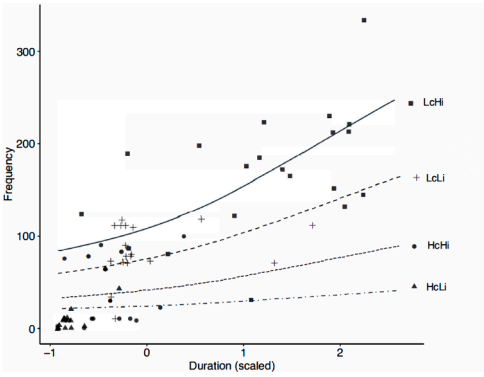

Fig. 3. Relationship between the scaled duration (mean = 0, SD = 1) spent in the test chamber and the frequency of visits in four treatments (LcHi, LcLi, HcHi, HcLi) in captive *Rhabdomys dilectus*. Points represent individual observations. Lines represent LOESS descriptive trendlines and are used here for illustrative purposes only and are not statistical models tested.

treatments. LOESS curves are shown to illustrate the general trends; however, these plots are descriptive and were not statistically tested.

3.3. Proportion of behaviours

Treatment significantly affected the proportion of time mice spent circuit running ($\chi^2 = 179.47$, df = 3, $p < 0.001$; Fig. 4). Circuit running was significantly higher in LcHi and HcHi treatments than in LcLi and HcLi treatments (Tukey post hoc comparisons, all $p < 0.001$). There was no significant sex effect ($\chi^2 = 1.75$, df = 1, $p = 0.186$).

For the other behaviours, treatment significantly affected digging ($\chi^2 = 163.63$, df = 3, $p < 0.001$). Digging was highest in the HcLi and LcLi treatments and lowest in the LcHi and HcHi treatments (Tukey post hoc, $p < 0.001$; Fig. 5). Sex was not a significant predictor of digging (c2 = 0.45, df = 1, $p = 0.502$). Treatment significantly affected exploratory behaviour ($\chi^2 = 19.70$, df = 3, $p < 0.001$), being greatest in the LcLi and HcLi treatments compared to the LcLi and HcLi treatments, followed by the LcHi and HcHi treatments (Tukey post hoc, $p < 0.001$; Fig. 5). Sex was not a significant predictor of exploration (c2 = 0.01, df = 1, $p = 0.929$). Treatment significantly influenced inactivity ($\chi^2 = 48.56$, df = 3, $p < 0.001$). The LcHi and HcHi treatments displayed lower proportions of inactivity compared to the HcLi and LcLi treatments (Tukey post hoc, $p < 0.001$; Fig. 5). Sex was not a significant predictor of inactivity (c2 = 2.36, df = 1, $p = 0.125$). Treatment significantly affected other behaviours ($\chi^2 = 55.61$, df = 3, $p < 0.001$). The LcLi and

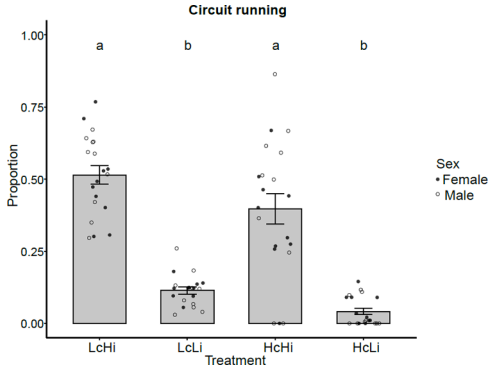

Fig. 4. Mean (± SE) proportion of time spent performing circuit running behaviour in four treatments (LcHi, LcLi, HcHi, HcLi) in captive *Rhabdomys dilectus*. Individual data points are shown, with females shown as solid circles and males as open circles. Different letters above bars indicate statistically significant differences between treatments (Tukey post hoc comparisons, $p < 0.05$).

HcLi treatments displayed more other behaviour that the LcHi and HcHi treatments (Tukey post hoc, $p < 0.0015$; Fig. 5). Sex was not a significant predictor of inactivity (c2 = 2.36, df = 1, $p = 0.125$).

Table 1 shows the demand for circuit running behaviour at varying costs. The demand for circuit running behaviour was determined by the duration, analogous to how sales of an item signify its demand (need). In other words, the 'cheapest' treatment ('best value for money') is LcHi because the animal gains the highest incentive while paying the lowest cost. Conversely, the most 'expensive' treatment is HcLi, where the animal gains a nominal incentive for a high cost. Pairwise comparisons of treatments showed that the relationship between LcHi and HcLi was elastic, with a 1 % change in cost resulting in a 1.190 % change in the proportion of circuit running behaviour. The relationship between LcHi and HcHi was inelastic, with a 1 % change in cost resulting in a 0.100 % change in the proportion of stereotypical behaviour. The comparison between LcHi and LcLi also showed an elastic relationship, with a 1 % change in cost leading to a 1.911 % change in the proportion of circuit running behaviour. The relationship between LcLi and HcLi was inelastic, with a 1 % change in cost resulting in a 0.930 % change in the proportion of circuit running behaviour. The comparison between LcLi and HcHi showed the greatest level of elasticity, with a 1 % change in cost resulting in a 3.329 % change in the proportion of circuit running behaviour. Finally, the relationship between HcLi and HcHi was also elastic, with a 1 % change in cost leading to a 2.590 % change in the proportion of circuit running behaviour. Overall, the elasticity scores and proportions of circuit running behaviour were consistent. Higher elasticity scores generally corresponded to higher proportions of circuit running behaviour (Fig. 4) related to costs (pipe length and test chamber size), indicating that treatments with higher responsiveness also had higher costs because of the length of pipe and reduced incentive (Table 1). Comparisons with inelastic outcomes (elasticity score < 1) were less responsive to changes in cost (Table 1), and the proportion of circuit running behaviour was similar (Fig. 4).

4. Discussion

We investigated whether circuit running behaviour in African striped mice *Rhabdomys dilectus* is a coping response or a flexible response to captive conditions, using a consumer demand approach. We found that circuit running demand was predominantly elastic: striped mice reduced performance when the energetic cost of accessing suitable running space increased. Striped mice spent more time and performed a higher proportion of circuit running when the incentive (available space) was high and the cost (pipe length) was low (LcHi treatment). As costs increased, either via longer travel distances or reduced incentive value, both the total time spent and the performance of circuit running declined. These patterns are consistent with an elastic demand curve, suggesting that circuit running is a flexible, cost-sensitive behaviour rather than an essential necessity.

Two pairwise comparisons (LcHi vs HcHi; LcLi vs HcLi) indicated inelastic demand, where pipe length alone did not strongly affect circuit running when incentive size was kept constant. However, these inelastic effects were small relative to the overall pattern of elasticity observed across treatments and must be considered within the context of the costs incurred, for several reasons. First, the mice spent the most time in the test chamber in the LcHi treatment, which was 6.1 times greater than in the HcHi treatment and 34.7 times greater than in the HcLi treatment. The mice appeared to have maximised the reduced time in the HcHi and displayed a similar proportion of circuit running behaviour to the LcHi treatment. Second, the reduced time in the test chamber resulted in a 3.9 times overall reduction in the absolute duration of circuit running: a median of 1853.5 seconds in LcHi versus 481.4 seconds in HcHi. Third, the proportion of circuit running was traded off against digging, inactivity, exploration and other behaviours in the LcHi, LcLi, and HcLi treatments; when circuit running was costly to perform, the proportion of non-circuit running behaviours increased. A similar pattern was

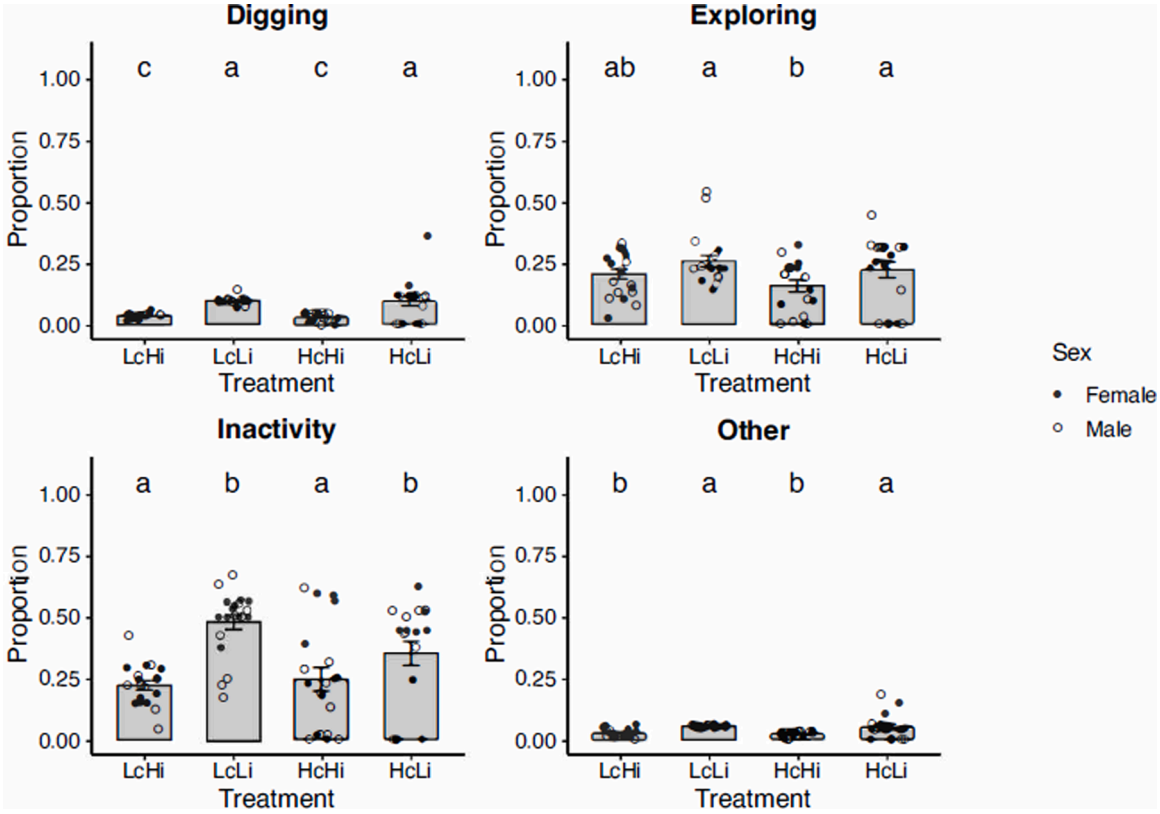

Fig. 5. Mean (± SE) proportion of time spent Digging, Exploring, Inactivity and Other behaviours in four treatments (LcHi, LcLi, HcHi, HcLi) in captive *Rhabdomys dilectus*. Individual data points are shown (females: solid circles; males: open circles). Different letters above bars denote significant differences (Tukey post hoc tests, $p < 0.05$).

Table 1
Pairwise comparisons of elasticity score and outcome (elastic vs inelastic) between four treatments: LcHi (Low-cost, High-incentive); LcLi (Low-cost, Low-incentive); HcHi (High-cost, High-incentive); and HcLi (High-cost, Low-incentive).

Comparison	Cost	Elasticity score	Elasticity outcome	Interpretation
LcHi vs HcLi	1 vs 6	1.190	elastic	Pipe length and test chamber size influenced circuit running behaviour
LcHi vs HcHi	1 vs 3	0.100	inelastic	Pipe length did not influence circuit running behaviour
LcHi vs LcLi	1 vs 2	1.911	elastic	Test chamber size influenced circuit running behaviour
LcLi vs HcLi	2 vs 6	0.930	inelastic	Pipe length did not influence circuit running behaviour
LcLi vs HcHi	2 vs 3	3.329	elastic	Pipe length and test chamber size influenced circuit running behaviour
HcLi vs HcHi	3 vs 6	2.590	elastic	Test chamber size influenced circuit running behaviour

evident in the HcHi treatment, although mice also decreased exploratory behaviour, thereby investing a greater proportion of in the limited time available in circuit running. Fourth, the relationship between the duration of time spent and frequency of visits to the test chamber was strong and positive in the LcHi treatment, but weaker and more variable in the HcHi treatment, indicating that the mice visited the test chamber less often and for more variable durations when cost increased. Thus, while pipe length alone did not fully suppress motivation when incentive value was high, the overall decrease in time spent, visit frequency and behavioural diversity indicates that the energetic burden was sufficient to influence behaviour. These results suggest that circuit running is sensitive to external costs and may not represent a fixed behavioural output associated with coping.

Our findings challenge interpretations of circuit running as a stereotypical behaviour maintained solely by neurological dysfunction. Repetitive behaviours, considered as stereotypical behaviours, in other species, such as veal calves (Wiepkema et al., 1987), bank voles *Clethrionomys glareolus* (Ödberg, 1987; Schoenecker, 2009), and mice (Würbel et al., 1998; Würbel and Stauffacher, 1999), have been associated with altered welfare states or neurobiological changes. Neural dysfunctions, as proposed for basal ganglia involvement (Garner et al., 2003; Mason, 2006), or from persistent internal motivation when natural behaviours are frustrated (Mason and Latham, 2004; Mason, 2006), often leads to fixed routines that cannot be disrupted (Garner et al., 2003; Würbel and Stauffacher, 1997; Vickery and Mason, 2005), In contrast, our behavioural evidence in *R. dilectus* suggests that circuit running is flexible and environmentally responsive. We are mindful, however, that without direct data, we cannot conclusively determine underlying neurobiological mechanisms.

Elastic behaviours, although flexible, still have functional significance. They may serve as substitutes for thwarted natural behaviours, opportunities for self-stimulation and/or strategies to modulate arousal levels (Mason, 1991; Mason and Latham, 2004). In captivity, where challenges such as foraging or predator avoidance are absent (McFarland, 1989), animals often experience excess available time (Hughes and Duncan, 1988) and energy (Würbel, 2001), which may promote the development of repetitive behaviours. In this context, circuit running in *R. dilectus* may function as a facultative time-filling activity rather than representing a mandatory coping strategy. This interpretation is consistent with broader findings that stereotypical behaviours may not always be reliable welfare indicators. In some cases, stereotypic animals exhibit higher survival or reproductive success than non-stereotypic counterparts, as reported in bank voles (Schoenecker,

2009) and in striped mice (Jones et al., 2008). Thus, while stereotypical behaviour often signals a suboptimal environment, it can also be part of a broader behavioural repertoire that offers coping-like benefits without necessarily indicating poor welfare.

5. Conclusion

Circuit running behaviour in captive African striped mice *Rhabdomys dilectus* displays characteristics of a luxury, not a necessity, under the framework of consumer demand theory. The flexible, cost-sensitive expression of this behaviour suggests that it does not function as an essential coping mechanism but may instead represent a facultative time-filling activity within the constraints of the captive environment. Our study focused exclusively on individuals expressing circuit running, which may limit generalisability to other contexts. Future research should compare cost-sensitivity among individuals with and without repetitive behaviours and incorporate direct physiological or neurobiological measures to clarify the motivational and the welfare implications of circuit running broadly. Finally, our findings highlight the value of economic models for assessing the motivational basis of behaviour and contribute to a more nuanced understanding of repetitive behaviour in captive animals. Broadening this approach across species and behavioural phenotypes offers promising avenues for future research into behavioural flexibility, welfare and adaptation to captivity.

CRediT authorship contribution statement

Kirsty-Jane Hartman: Writing – original draft, Project administration. **Sneha Joshi:** Writing – review & editing, Conceptualization. **Neville Pillay:** Supervision.

Declaration of Competing Interest

The authors declare no conflict of interest.

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The authors declare no conflict of interest.

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