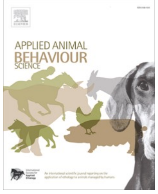
Applied Animal Behaviour Science 271 (2024) 106167

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

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



Animals with various forms of abnormal behaviour differ in learning performance and use of enrichment: Evidence from farm mink

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ARTICLE INFO

Keywords:
Abnormal behaviour
Cognition
Fur-chewing
Learning
Neogale vison syn. Neovison vison syn. Mustela vison
Stereotypic behaviour

ABSTRACT

Abnormal behaviour has been related to differences in cognitive function and reduced animal welfare. However, these associations are understudied, and little is known about how various forms of abnormal behaviour affect learning performance, stress responses and use of enrichment. We tested the hypotheses that different forms of abnormal behaviour are (1) associated with various degrees of impairment of learning, (2) generally related to elevated stress responses including fearfulness, and (3) reduced during periodical access to running wheels using American mink (*Neogale vison*, synonym *Neovison vison*) as model species. Farm mink were screened into groups displaying no apparent abnormal behaviour (NONE, n=35), or abnormal behaviour as fur-chewing (FURCHEW, n=21), Stereotypic Behaviour (SB) i.e., pacing (PACERS, n=33), stationary SB (STATSB, n=22), licking SB (ORALSB, n=17), and combination of forms (MIXED, n=22). Learning performance was assessed in a two-choice visual discrimination test with three progressive stages: 94% passed the 1st (acquisition), 70% the 2nd (recall) and 42% the 3rd (reversal) stage. Mink from groups MIXED and PACERS passed more learning stages than ORALSB and NONE mink (MIXED 2.3^{a}; PACERS: 2.1^{a}; ORALSB 1.4^{b}; NONE: 1.4^{b}, $F_{5,83}$=2.7, P=0.027), while the other groups did not differ significantly (STATSB: 1.9^{ab}, FURCHEW: 2.0^{ab}). Thus, the most locomotory active forms of abnormal behaviour appeared associated with enhanced learning. NONE mink spent more time in investigative sniffing (13 ±1.6 s) than did mink with abnormal behaviour (6 ±0.9 s) in a 30 s temperament test ($F_{5,144}$=3.2, P=0.010). A large individual variation in faecal cortisol metabolite levels rendered this indicator insensitive to detect group differences. When given access to a running wheel, the groups differed in activity ($F_{5,131}$=10.0, P<0.001): Revolutions per day, MIXED: 1929^{a}, STATSB: 1445^{a}, PACERS: 1435^{ab}, ORALSB: 466^{bc}, FURCHEW: 485^{c}, and NONE: 344^{c}. All forms of SB, except licking, were significantly reduced (P<0.001) during running wheel access. Thus, licking SB appears different from the other SBs. In conclusion, different forms of abnormal behaviour appear associated with different cognitive and motivational characteristics. Further, our results suggest a potential positive link between physical activity (even if it is stereotypic) and learning.

1. Introduction

Abnormal behaviour occurs relatively frequently in millions of farm, pet, and zoo animals. These types of behaviour have puzzled the stand-by-viewers, caretakers and researchers for decades: why this strange behaviour and what are the consequences for the individual performing this behaviour? Theories behind the development of abnormal behaviour focus on species-specific motivations (e.g. Mason and Mendl, 1997). Thwarted motivated behaviour under barren housing may lead to the development of abnormal behaviour (Hughes and Duncan, 1988) and stress (Jensen and Toates, 1997). However, individual variation exists, not only in the propensity but also in the form of abnormal behaviour developed in e.g. farm animals. Farm mink (*Neogale vison,* synonym *Neovison vison*) which are bred, fed, and managed under equal conditions display a range of abnormal behaviours such as fur-chewing (oral hair removal, tail-sucking) and stereotypic behaviours (SB). Bildsø and co-workers (1991) described ten different types of SB in farm mink. However, despite a variation in the behavioural display, SB is often pooled into a few classes to facilitate feasible sampling and analysis (e.g. pacing vs. non-pacing or stationary), occasionally supplemented with borderline cases, i.e. behaviour not meeting the authors' criterion of three to five uninterrupted, consecutive repetitions (Hansen et al., 2007;

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https://doi.org/10.1016/j.applanim.2024.106167
Received 26 October 2023; Received in revised form 4 January 2024; Accepted 11 January 2024

Svendsen et al., 2007; Dallaire et al., 2011, 2012; Campbell et al., 2013). Polanco and co-workers (2017) reported differences between mink 'head-based' (stationary form) versus a pool of 'whole-body' locomotory forms of SB, the latter being correlated to route-pacing.

Additionally, scrabbling with forepaws at cage inventory is listed as a potential SB in mink (Dallaire et al., 2011, 2012; Campbell et al., 2013). The nature of scrabbling is still under exploration and was related to different triggers (Diez-Leon et al., 2013; Polanco et al., 2017, 2018) and neurophysiological correlates (Diez-Leon et al., 2019) than pacing SB. Pacing is considered the most prevalent form of SB in farm mink (Hansen et al., 2007; Svendsen et al., 2007) – estimated to be roughly 60% of SB observations in (Clubb and Mason, 2007) – although fur-chewing and other SB forms were also reported at the same farm, in mink with equal heritage, housing and management conditions (Malmkvist et al., 2013).

Previously, large-scale studies documented a higher baseline cortisol in stereotypic mink (Hansen and Jeppesen, 2006; Svendsen et al., 2007). Further, highly stereotypic mink reacted with higher cortisol in response to handling, compared to non-stereotypic mink (Hansen and Jeppesen, 2006). Likewise, a smaller study linked stress with SB; the performance of stereotypies increased following stressors such as handling/immobilisation and food restriction, and highly stereotyping mink reacted with higher blood cortisol responses to a standardised stressor (Bildsø et al., 1991). Overall, mink performing stereotypic behaviour appear to be characterised by an increased reactivity to stressors.

The association between abnormal behaviour and other indicators of stress and reduced welfare are, however, not always straightforward. One study reported, for example, that stereotyping mink females were less fearful and more explorative (i.e. reacted with less flight and more sniffing) than non-stereotyping females during a voluntary approach test (Hansen and Jeppesen, 2006), though not significantly different in a follow-up study (Svendsen et al., 2007). Further, although long-term stress potentially inhibits adult hippocampal neurogenesis in a range of mammals (Balu and Lucki, 2009), brain hippocampal cell proliferation was unexpectedly found to increase with increasing performance of SB in adult mink (Malmkvist et al., 2012). This may be in line with findings in mice, in which enhanced neurogenesis via both increased cell proliferation and cell survival in the adult hippocampus were induced by voluntary exercise in running wheels (van Praag et al., 1999). Both exercise and locomotory SB, such as pacing, involve elevated physical activity and may therefore be beneficial for neurogenesis. In the current study, we quantified running wheel activity in mink with abnormal behaviour of a relatively passive (fur-chewing, licking SB), intermediate (stationary SB) or highly active (pacing, mixed) nature as well as in mink that were not observed to show abnormal behaviour.

The impact of abnormal behaviour on aspects of cognition and learning performance has been studied across species, e.g. laboratory rodents (Garner and Mason, 2002), mink (Dallaire et al., 2011; Campbell et al., 2013), and horses: (Hausberger et al., 2007; McBride and Parker, 2015; Freymond et al., 2019), but results are varying. We hypothesise a potential CNS dopaminergic dysfunction and reduced cognitive flexibility in animals with abnormal behaviour as previously suggested (Garner and Mason, 2002; McBride and Parker, 2015). Thus, we predict impaired reversal learning in mink with abnormal behaviour. However, we do not expect mink with abnormal behaviour to show a general reduction in the acquisition phase, as the signs of enhanced hippocampal health in farm mink with high levels of physical activity due to stereotypic behaviour (Malmkvist et al., 2012) could favour their learning performance, as hippocampal function governs learning and memory (Lupien et al., 1998).

Overall, the understanding of abnormal behaviour and its correlates is rudimentary. Further, it is worth considering whether inactive (i.e., non-stereotypic) farm animals are e.g. bored, apathetic or frightened rather than in a relaxed state (debated in Meagher et al., 2013; Meagher et al., 2017; Meagher, 2019).

We aimed to contribute to the understanding of the diversity of abnormal behaviour, including a group of mink which did not show abnormal behaviour. We tested the hypotheses that different forms of abnormal behaviour in farm mink are (1) associated with various degrees of impairment of learning and reversal learning, (2) generally related to elevated stress responses including fearfulness, and (3) variably reduced during periodical access to running wheels.

2. Materials and methods

2.1. Animals, housing and management

The study took place at the experimental farm at Aarhus University (AU; DK-8830 Tjele, Denmark) between the months of October-December 2019. Female mink were selected for this study from a breeding stock of 1151 adult brown (80.6%) and palomino (19.4%) mink females, outside the reproductive season. The mink were individually housed in cages measuring 30 ×45×90 cm (W x H x L) as common practice. All cages were provisioned with a straw-bedded wooden nestbox outside the cage (28 ×20×23 cm), as well as a shelf at the back of the cage (30 ×16 cm, raised 30 cm from the cage floor) and a plastic cylinder (32 cm long, diameter 10 cm, allowing for mink access) as enrichment items, as mandatory for the keeping of mink in Denmark (Danish Ministry of Environment and Food, 2015). The mink were fed once daily with commercial mink feed (from Hvalpsund feed factory, DK-9640 Denmark), and water was provided *ad libitum* via nipple drinkers. Feeding time varied between 10:30 and 13:00 but was kept constant within the different phases of the experiment (i.e. 13:00 during screening observations and learning trials, 11:00 during direct observations of behaviour; see timeline Fig. 1). All observations occurred pre-feeding; as typical for carnivores (Mason and Mendl, 1997), mink perform most of their SB pre-feeding (Hansen et al., 1994; Malmkvist et al., 2013). Mink were housed in sheds exposed to natural lighting and ventilation. The experimental mink were before the first relocation scattered around the research farm facility, but after the relocation part of the study collected in two sheds, and then housed in a mixed order avoiding same-group neighbours.

2.2. The experimental groups

A timeline of the experimental protocol and the sample size for the different parts is shown in Fig. 1. In the first phase, the adult mink females (N=1151) were screened to identify individuals displaying abnormal behaviour, in terms of SB and fur-chewing, for the creation of experimental groups. The second phase consisted of data collection (temperament test, learning performance, FCMs and behaviour associated with relocation to novel cage, and running wheel activity) on mink allocated to the six experimental groups.

The initial screening took place October 7–11, from h 8–12 daily. Stereotypies, defined as repetitive, unvarying and apparently functionless behaviour (Mason, 1991), were one-zero sampled during four rounds (1 min per cage) per mink during the hours before feeding, resulting in a total of 20 rounds per mink. We observed two previously undescribed forms of mink SB in the present study: repeated non-nutritional licking on the cage wire (video supplementary information S1) and clapping with front paws while standing on the hind legs, which we categorised as an oral SB and a stationary SB, respectively. The types of abnormal behaviours identified were pacing SB (video supplementary information S2), stationary SB (including up-down bobbing, paw waving, clapping), oral SB (licking, biting not directed at the feeding mesh or drinking nipple), scrabbling with front legs, and mixed forms. Additionally, fur-chewing (photo supplementary information S3), which is the destruction of hair induced by sucking and gnawing (Malmkvist and Hansen, 2001), was scored over two days. Following this screening, candidate mink were selected for behavioural observation October 22–23, aiming to create groups of a minimum of 16 mink per behavioural phenotype. We were unable to create a consistent group of mink with scrabbling SB as this behaviour

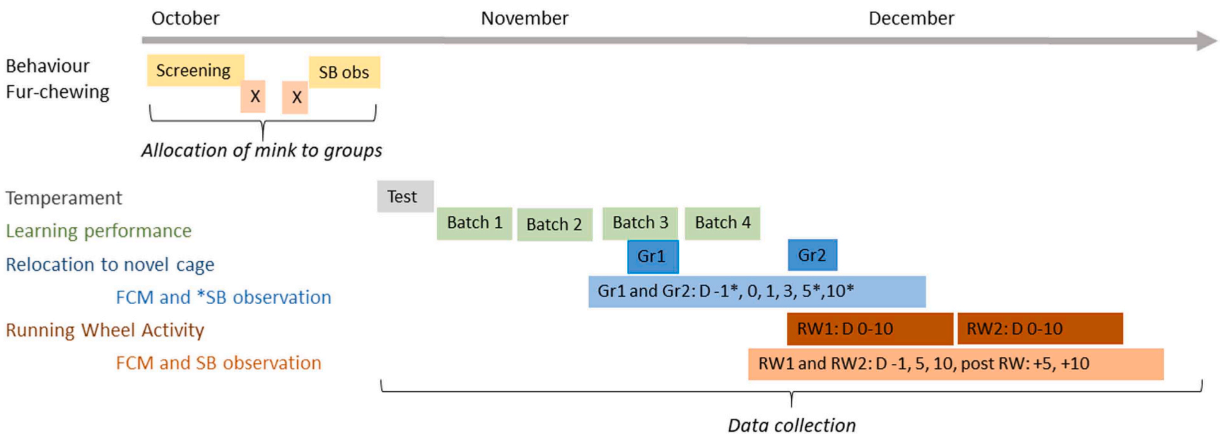

Fig. 1. Timeline for the experiment. Phase 1 from October 7–23 included the screening of 1151 adult female farm mink for allocation into groups displaying different forms of abnormal behaviour. Phase 2 from October 24-December 27 included the data collection: (1) test of temperament (n=150 mink), (2) learning performance in four 5-day batches (n=91 mink), (3) Sampling of faeces for analysis of cortisol metabolites (FCMs) and stereotypic behaviour (SB) observation relative to relocation to a novel cage in two batches (Gr1: n=75, Gr2: n=75 mink), and (4) Running wheel (RW) activity in two batches (RW1: n=44, RW2: n=44 mink). RW mink were sampled for FCMs and SB observation the day before (D −1), during (D 5, 10), and after (+5 and +10) the 10 days of wheel access.

declined/disappeared in mink as the observation days progressed. The resulting six groups (150 mink) showed fur-chewing (no SB observed, at least 2 cm of tail-chewing, range 2–9 cm; FURHEW, n=21), pacing (pacing as dominant SB, range 25–100% of observations, no fur-chewing; PACERS, n=33), stationary SB (stationary SB as dominant, range 38–100% of observations, no fur-chewing; STATSB, n=22), licking SB (licking observed as dominant SB, range 10–100% of observations, no fur-chewing; ORALSB, n=17), several forms (combinations of SBs, or one SB combined with at least 2 cm of tail-chewing; range pacing 0–100%, stationary SB 0–75%, oral SB 0–38% of observations, range fur-chewing 0–9 cm; MIXED, n=22) or free from abnormal behaviour (range of activities out in the cage 0–80% of observations; NONE, n=35).

Supplementary material related to this article can be found online at doi:10.1016/j.applanim.2024.106167.

We only included healthy adult female mink from the breeding stock and did not consider age class (1.5, 2.5 or 3.5 years) or colour type (Brown or Palomino) when creating the six groups. Table 1 summarises the behaviour of mink in the six experimental groups before the data collection. We excluded two mink from entering the RW part during the phase of data collection: one ORALSB mink was not observed performing licking stereotypies beyond October and one NONE mink developed 1 cm of fur-chewing in November, measured on the day of relocation to a novel cage.

2.3. Relocation procedure

All adult mink had to be moved to a novel cleaned cage due to farm practice this time of year. Therefore, after introducing standardisation, we used the relocation to test the minks' baseline FCM levels and responses to handling and movement to a novel cage, which we considered a mild stressor, cf. also (Bak and Malmkvist, 2020). The mink were caught in metal transport cages (L:61.5 x W:13.5 x H:14.5 cm, 2 M-Group, DK-6852 Billum, Denmark) and kept individually for 15 minutes in this small unit placed on top of their home cage, before being moved to a novel cage in another house within the farm. The novel cage was cleaned and of the same type as their original home cage, holding the same resources. The mink were moved in a balanced, randomised order in two batches of 75 mink (1: Nov 14, 2: Nov 26) at h 8–9. Fur-chewing was scored on each mink while in the transport cage. The mink were subsequently housed in a mixed way, avoiding same-group neighbours.

2.4. Running wheel access

To test the motivational basis of the different forms of abnormal behaviour, the mink were moved to cages where they could access a running wheel (supplementary information S4), as previously used for mink (Hansen and Damgaard, 2009). Cage dimensions and equipment (next box, shelf and tube) remained otherwise the same. The mink were allocated to these cages in a pseudo-random manner so that all experimental groups were represented and interspersed across the rows of cages to avoid location confounds. To reduce bias, the experimental group placed in each of the 44 cage units with running wheel access differed between batches 1 and 2. The mink were housed in RW cage units for 10 days (Day 0, at h 8–9), and then relocated back to their home cages on Day 11, at h 0730. The number of wheel turns was continuously recorded per second and stored in a computer with a sampling rate above 30 kHz. In addition, live observations and FCM sampling were performed the day before (Day −1), and on Day 5 and 10 of running

Table 1
Behaviour in the six experimental groups of 150 mink in total. SB: Stereotypical behaviour.

	In nest box	Active[1]	Licking SB	Stationary SB	Pacing SB	Scrab-ble	Fur-chewing	N Mink
NONE	9 [7;10]	1 [0;3]	0	0	0	0 [0;0]	0	35
FURCHEW	7 [6;8]	3 [1;3]	0	0	0	0 [0;0]	4 ±0.5	21
ORALSB	4 [1;5]	4 [3;7]	3 [2;7]	0 [0;1]	0 [0;0]	2 [1;2]	0	17
STATSB	2 [1;3]	6 [5;7]	0	5 [4;5]	0 [0;0]	0 [0;0]	0	22
PACERS	2 [1;2]	6 [6;8]	0 [0;0]	0 [0;0]	5 [3;6]	0	0	33
MIXED	2 [0;3]	6 [5;8]	0 [0;1]	2 [0;3]	4 [2;5]	0 [0;0]	2 ±0.6	22

Behaviour given as median [25%; 75% quartiles] counts during 8–10 2-min observations with 30-min intervals during pre-feeding hours over two days and fur-chewing as mean ±SE cm on the tail for adult female mink in October (n=150 mink in total).
[1] Active is any type of active normal behaviour out in the cage.

wheel access, as well as on Day 5 and Day 10 once back in their home cages without RW access.

2.5. Data collection

The timeline for data collection is illustrated in Fig. 1. All 150 mink were tested for temperament (described below) and relocated to a novel cage entering the data collection for FCMs and SB observation, whereas subsets entered the other parts of our study. The reason for not collecting data on all mink for learning performance (91 mink, i.e. 60.7%) and running wheel (RW) activity (88 mink, i.e. 58.7% tested) was a limitation of time and resources; two persons could manage the learning performance test with up to 24 mink during the 5 days per batch (see later), and we had equipped 44 cage units with running wheels at the research farm. The relocation to a novel cage took place 5–12 days after the last day of the 5-day learning test, and the onset of running wheel activity was on days 11–12 after the relocation to a novel cage for RW mink (cf. Fig. 1). Thus, the different data collections came in the same order and did not overlap for the individual mink.

The animal caretakers at the farm and the persons involved in the data collection (temperament test, learning performance, behaviour and FCMs around relocation and RW access) were blind to the group affiliation of the individual mink.

2.5.1. Temperament test

This voluntary approach-avoidance test was performed in the minks' home cage as described in (Malmkvist and Hansen, 2002), demonstrating generalisation of mink responses across multiple different tests. Briefly, the test person put a tongue spatula through the wire net in the upper part of the front lid section when the mink was in the cage (i.e. not in nestbox), and noted the animal's reaction as (1) explorative: if the mink displayed explorative behaviour, i.e. approached and sniffed the stick persistently; (2) fearful: if the mink fled and did not touch the stick; (3) aggressive: if the mink attacked and bit the stick forcefully; (4) indecisive: if the mink showed a mixture of responses, or no interest, and could not be placed in one of the first three categories. There was a fixed test duration of 30 s, and the duration of stick contact (either sniffing or biting) was measured to the nearest second, using a handheld computer (Psion Teklogix Workabout MX, Pulster, D-68181 Leimen, Germany).

2.5.2. Learning performance in a two-choice discrimination test

Learning performance was assessed in a two-choice discrimination test with three progressive stages: 1. acquisition, 2: recall, and 3: reversal. To pass each stage, the mink had to select the correct figure (see below) for 9 out of 10 subsequent trials. The mink passed each stage before progressing to the next, i.e. demonstrating acquisition learning before being tested for recall (stage 2), and passing recall to enter the test of reversal learning (stage 3). Each mink was tested for up to 5 consecutive days, with a maximum of c. 30 trials per day (deemed optimal in terms of sustained motivation during a pilot study). The 12–18 tested mink per group were distributed evenly into four batches (see Fig. 1 for timeline).

Learning trials were conducted between 8:00–13:00 (i.e. pre-feeding) by two test persons, one presenting the two figures at the front end of the cage and delivering punishment (air blow) upon incorrect choices and the other person delivering the reward at the other end of the cage and attracting the mink to this part of the cage before each presentation of the figures, to ensure a standardised starting point.

In an initial 10-trial training stage, only the correct (rewarded) figure was presented to the mink and they were rewarded for touching the figure with their nose through the front cage wire; the figures were either a white plastic circle (diameter 8 cm), presented to the left of their front cage or a blue plastic square (8 ×6 cm), presented to the right of the front of their cage, c. 15 cm apart (Fig. 2). Thus, both spatial (left, right) and visual (colour, shape and size) cues were combined. This was chosen because a pilot study (n=10 adult females outside this

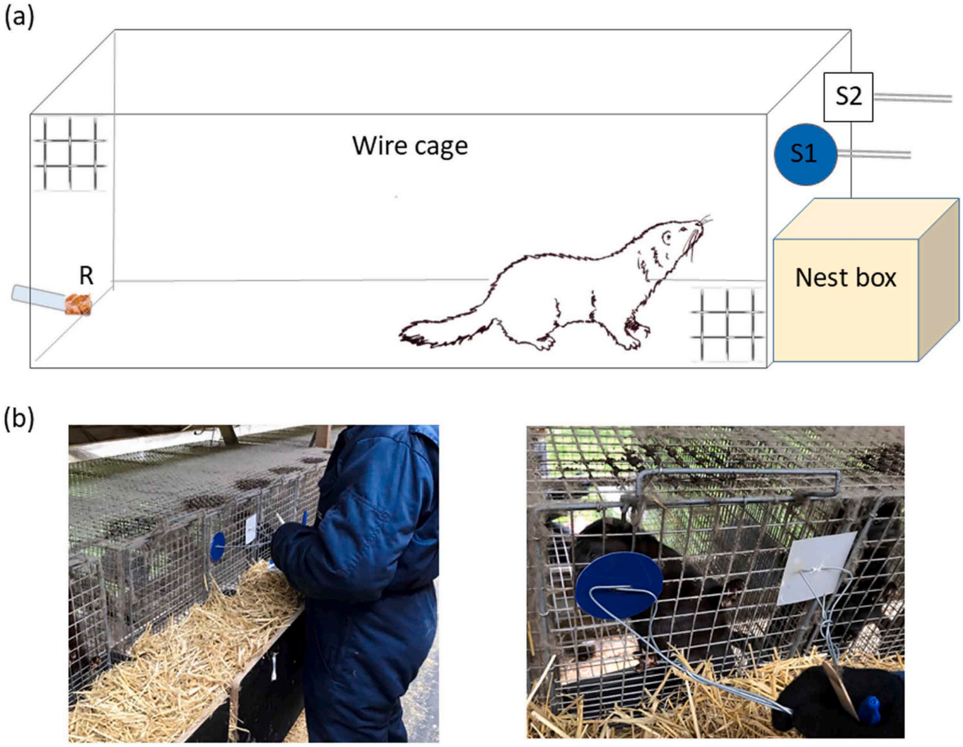

Fig. 2. Learning performance in a two-choice discrimination test. (a) Set-up and (b) mink in the home cage trained to choose between two figures (S1, S2), presented simultaneously by test person 1 above the nest box, vertically at the front lid of the wire cage facing the mink. Person 2 attracted the mink to the opposite part of the 90 cm long wire cage before each presentation of the figures (the standardised starting point). Person 2 delivered a reward (R) to the mink in case of a correct choice during the trial, i.e. if the mink touched the figure predetermined as correct. Person 1 provided an air puff to the face of the mink in case of an incorrect choice.

experiment) suggested that this discrimination task was readily learned by mink. The rewarded position/figure (hereafter termed figure) was counterbalanced between and within experimental groups. After the initial 10-trial training stage, the two figures were presented simultaneously to the mink. When the mink touched a figure with its nose, both figures were withdrawn immediately and if the choice was correct, they received a food reward (approx. 1 g of palatable cat wet food; Sheba Selection chicken) in the other end of the cage using a spatula (Fig. 2). In this manner, food treats were delivered as far as possible from the front of the cage, and also equidistant from the two figures. Incorrect choices were punished with an air puff directed towards the mink's face, which mink find mildly aversive, as determined in the pilot study. The mild punisher was included because the pilot study suggested that investigation of the figures may be rewarding in itself, as some mink continued to approach the figures for >50 presentations without any additional reinforcement. Thus, the inclusion of the mild punisher was considered necessary to motivate the mink only to choose the food-rewarded figure.

In the second stage (recall), mink that had passed the acquisition criterion (9 correct in 10 subsequent trials) were re-tested the following day, with the same rewarded stimulus. The recall criterion was 9 correct choices in the first 10 trials. This criterion ensured that the mink were reliably choosing the rewarded over the punished stimulus. If the mink passed this criterion, it immediately moved on to the reversal stage. If the mink did not pass, they received further trials (up to 30 per day) until passing the 9 of 10 criterion again, and they were then tested for recall again on the following day. No mink moved on to the reversal stage before passing the recall stage. In the third stage (reversal), mink passing stages 1 and 2 were exposed to a shift of rewarded/punished stimulus, i.e. the previously rewarded figure was now punished and the other was rewarded.

2.5.3. *Determination of faecal cortisol metabolites (FCMs)*

Fresh faeces were collected from beneath the defecation zone of individual cages using wire nets for both the relocation part and the RW part (Fig. 1). We sampled hours 11–17 on D −1, D0, D1, D3, D5, and D10 relative to the day of relocation to a novel cage (D0), and on D-1, D5, and D10 plus post RW D+5, and D+10 relative to the day of first RW access (D0); i.e. we determined FCMs before, during and after the 10 days of having access to RW.

FCMs have been validated for female mink and reflect concentrations of circulating cortisol with a time lag of approximately 4 h (Malmkvist et al., 2011). Samples (0.50 g) were stored at −20 °C until analysis at the laboratory at Aarhus University. The faecal sample was extracted with 5 ml (80%) ethanol and FCMs were measured in the supernatant with an 11ß-hydroxyaetiocholanolone enzyme immunoassay (EIA). The sensitivity of the method was 5 ng/g with intra- and inter-assay coefficients of variations of respectively 7.5 and 12.9% for low control (103 ng/g) and 11.2 and 12.8% for high control (319 ng/g).

2.5.4. *Determination of SB – behavioural observation*

Behaviour was observed (cf. description in supplementary information S5) on D-1, D5, and D10 relative to the day of relocation to a novel cage (D0), and on D-1, D5, and D10 plus post RW D+5, and D+10 relative to the day of first RW access (D0); i.e. we determined SB before, during and after the 10 days of wheel access.

On observation days, behaviour was observed for 2 min per cage during five rounds with 30 min intervals from hours 9–11 (i.e. pre-feeding). On D0, observation began at the earliest 1 h after the mink arrived at the novel cage, to standardise duration for habituation and time relative to feeding, which was delayed until 3 h after arrival to the new cage. Each mink was continuously scored for location and behaviour. Additionally, high-pitched vocalisations, scrabbling with front legs, and biting in the wire cage were counted.

We tested the intra- and inter-observer repeatability of the six trained observers collecting the data (according to ethogram, supplementary information S5); this was done by live-scoring 2-min video recordings of 15 mink selected from the experimental groups, presented twice in random order. Pearson correlation coefficients, r_p, was 0.98–1.00 within and 0.97–1.00 between the observers for location and behaviour. Thus, the duration of location and behaviour of the mink observed (in seconds) were highly correlated both within and between observers.

2.6. *Ethical considerations*

The experiment was conducted according to the Danish legislation, including the legal acts on protection of farmed fur animals (Danish Ministry of Environment and Food, 2015) and animal experimentation (Danish Ministry of Food, Agriculture and Fisheries, 2022). The study was below the permit-requiring threshold, as specified in the Danish animal experimentation law §2: use of animals expected to "cause pain, suffering, anxiety, or permanent injury equal to, or greater than, that caused by the injection of a needle, done in accordance with good veterinary practice" [translated from Danish], see also Nielsen et al. (2023). The sampling was of a non-invasive nature, interactions in the temperament test, learning task and with the running wheel were voluntary (not forced) for the animals, and no harmful handling was used. The study used an already planned relocation of the mink (part of the farm's yearly cleaning procedure) as a stressor. Benefits, such as the possibility for rewards and enrichment, were included for the involved farm mink.

2.7. *Statistical analyses*

A template ANOVA model (1) was used for analysing repeatedly measured response variables:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + R_{ijk} + \varepsilon_{ijk} \tag{1}$$

where μ is the general level; α_i is the effect of groups (i = NONE, FURCHEW, ORALSB, STATSB, PACERS, MIXED); β_j is the effect of the day (j from −1 to +10, cf. Fig. 1), $(\alpha\beta)_{ij}$ is the interaction between group and day; R_{ijk} is the repeated effect (k = 1…N), with N = 150 mink for the full data; and ε_{ijk} is the residual part. The statistical software SAS (version 9.4) was used for calculations (procedure MIXED unless otherwise stated). The time structure was modelled using compound symmetry as it resulted in the best fit according to Akaike's Information Criteria and Bayesian Information Criteria (AIC and BIC in SAS). The Kenward-Roger approximation was used for the denominator degrees of freedom.

The template model was modified to meet the conditions of the sampled data as described in the following. The stick test data (scores, duration of contact) were analysed in a model similar to model (1), without day and the repeated statement as only measured once. The scores in the temperament test were analysed as binomial in a generalized linear model (procedure GENMOD in SAS), except for 'fearful' observed in only three out of the 150 adult mink (2%). For the learning performance (number of passed stages, trials to pass each stage for the first time), the initial rewarded figure (blue circle or white square) was included as a factor in the model, without day and the repeated statement as only measured once. The trials to pass each stage for the first time (1. Acquisition, 2. Recall, 3. Reversal) were analysed using survival analysis considering censored data (Klein and Moeschberger, 2003) as 5.6% (stage 1), 29.8% (stage 2) and 57.6% (stage 3) of the mink did not pass before the time-out/maximum number of trials. This survival analysis was based on a Cox regression model (PHREG procedure in SAS), as the assumption on proportional hazard rates between groups (over trials) could not be excluded based on plots of the survival curves. The FCM data were log-transformed as this improved the model residuals and analysed in the model (1) extended with the time of faecal sample (h 11–17) and noon outdoor temperature (1.8–9.9 °C) within days as covariates. For data from direct observations (relative to relocation to a novel cage, and periodical RW access), continuous observations of location and behaviour (supplementary Information S5) were analysed as the proportion of observation time in the model (1) extended with noon outdoor temperature as covariate. The time spent in licking, stationary and pacing SB were log-transformed as this improved the model residuals. Specifically for behaviour in relation to RW access, days in the statistical model were replaced by 3 periods; before (day −1), during (days 5 and 10) and after (days 15 and 20) the periodical RW access (cf. Fig. 1), justified by plots of data per day. Counts were analysed with a negative binomial distribution (procedure GLIMMIX in SAS), reducing the risk of overdispersion, evaluated as the model Pearson Chi-Square/DF approximating to 1. Fur-chewing was analysed in a model similar to the template model (1), without day and the repeated statement as only measured once. Running wheel activity (revolutions per second) were summed to revolutions per day (rpd, 24 h) and log-transformed for the analysis.

Models were reduced by stepwise removal of insignificant terms ($P > 0.10$), starting with the interaction and otherwise removing the term with the highest P-value first. Factors with $P \leq 0.10$ and the fixed factor of the study (α_i: groups) were always kept in the model. For the ANOVAs based on normally distributed data (the procedure MIXED in SAS), the compliance with dispersion and variance homogeneity was verified by visual inspection of residual plots at each step in the model reduction and for the final model. The probability level (P) ≤ 0.05 was chosen as the limit of statistical significance in all tests, with results between $0.05 < P \leq 0.10$ reported as tendencies. Fisher's least significant difference (LSD) was used for post-tests, i.e. for pairwise comparison in case of a significant fixed factor with more than two levels. All statistical tests are two-tailed. Means of raw data are reported ±standard error unless otherwise stated.

3. Results

3.1. Learning performance in a two-choice task

The number of stages passed differed between groups ($F_{5,83} = 2.7$, $P = 0.027$). Mink in groups PACERS and MIXED passed on average more stages (2.1–2.3) than mink in groups ORALSB and NONE (1.4; Table 2). This result suggests differences in learning performance, rather than variation in motivation to participate, as the groups did not differ in the total number of trials taken ($F_{5,\ 83} = 1.2$, $P = 0.33$; Table 2). Two NONE mink were given up as not willing to participate; one mink took zero rewards in one trial, and another mink took two rewards during three trials, before stopping and withdrawing into the nest box. However, the rest worked well and took the reward treat offered in the two-choice learning task. The majority (94.4%) of the 89 tested mink reached the learning criterion of nine correct out of 10 choices in the acquisition stage 1, whereas the proportion was lower for recall the next day (70.2% for stage 2) and for reversal learning (42.4% for stage 3; supplementary information S6). Analysing the different stages (1: acquisition, 2: recall, 3: reversal) separately, there was no significant difference between groups in the number of trials used to pass (Survival Analysis, stage 1: $\chi^2_5 = 5.2$, $P = 0.39$, 5.6% censored; stage 2: $\chi^2_5 = 6.0$, $P = 0.30$, 28.1% censored; stage 3: $\chi^2_5 = 2.8$, $P = 0.74$, 57.6% censored; supplementary information S6). As expected, the type of reward figure (blue circle or white square; cf. Fig. 2) did not influence the speed of learning (stage 1: $\chi^2_1 = 0.6$, $P = 0.43$; stage 2: $\chi^2_1 = 0.8$, $P = 0.37$, stage 3: $\chi^2_1 = 0.9$, $P = 0.34$).

Table 2
Performance of mink (n=89) in the two-choice visual discrimination task.

	Stages passed	Total trials	Rewarded trials, %	N mink
NONE	1.4 ±0.18 (0–3)^{a}	90 ±7.9 (38–151)	60 ±2.2 (40–74)	16
FURCHEW	2.0 ±0.26 (0–3)^{ab}	94 ±10.5 (36–158)	63 ±2.2 (49–76)	12
ORALSB	1.4 ±0.30 (0–3)^{a}	110 ±8.9 (32–153)	56 ±1.8 (44–68)	13
STATSB	1.9 ±0.17 (1–3)^{ab}	108 ±8.3 (30–167)	63 ±2.8 (46–97)	18
PACERS	2.1 ±0.19 (1–3)^{b}	113 ±8.5 (40–170)	61 ±2.5 (43–93)	18
MIXED	2.3 ±0.22 (1–3)^{b}	107 ±7.4 (57–149)	54 ±2.1 (40–67)	12
Test statistics	$F_{5,83} = 2.7$	$F_{5,83} = 1.2$	$F_{5,83} = 1.9$	
P-value	0.027	0.33	0.10	

Results as mean ±se (range) stages passed, total number of trials and proportion of rewarded trials in the two-choice learning test with three progressive stages. abDifferent letters indicate a significant difference between groups, $P \leq 0.05$.

3.2. Temperament in the stick test

The proportion of mink that scored 'explorative' averaged 39% and differed between the groups ($\chi^2_5 = 11.6$, $P = 0.041$). A higher proportion of NONE (57%^{a}) and ORALSB (47%^{a}) mink were 'explorative' than mink in groups PACERS (27%^{b}) and FURCHEW (14%^{b}) during the stick test, with groups STATSB (41^{ab}) and MIXED (41^{ab}) not being statistical different ($P > 0.05$) from the rest. Only three out of the 150 adult mink (2%) were assessed 'fearful' in the stick test. The rest of the adult female mink were categorised as 'aggressive' (29%) or could not be categorised (31% 'indecisive'), and were not differently distributed between the groups ('aggressive': $\chi^2_5 = 4.3$, $P = 0.51$; 'indecisive': $\chi^2_5 = 4.8$, $P = 0.44$).

The groups also differed in the duration of explorative contact measured during the test ($F_{5,\ 144} = 3.2$, $P = 0.010$). The NONE mink spent on average 1.6–2.6 more time sniffing/investigating the stick than did mink from any of the groups with abnormal behaviour (s: 13 ±1.4^{a} vs. 5 ±1.8^{b} in FURCHEW, 7 ±2.0^{b} in ORALSB, 8 ±1.8^{b} in STATSB, 7 ±1.5^{b} in PACERS, and 8 ±1.8^{b} in MIXED mink). The duration of the mink biting the stick aggressively (9 ±1.0 s) did not differ between groups ($F_{5,\ 144} = 1.5$, $P = 0.20$).

3.3. FCM baseline and response to relocation to a novel cage

There was no difference between groups in Faecal Cortisol Metabolite (FCM) baseline, i.e. sampled in the home cage the day before relocation to a novel cage ($F_{5,\ 124} = 0.5$, $P = 0.76$). Likewise, there was no difference between groups in FCM response after relocation to a novel cage, day 0–10 (supplementary information S7; Group: $F_{5,\ 138} = 0.4$, $P = 0.87$; Day: $F_{4,\ 546} = 0.2$, $P = 0.93$; Group*Day: $F_{20,\ 512} = 0.9$, $P = 0.60$). The variation in FCMs was large between mink (range 2–5027 ng/g), making it difficult to detect group and day differences in the present study. The FCM decreased with sampling hour (range h 11–17; baseline: $F_{1,\ 124} = 8.s0$, $P = 0.006$; response: $F_{1,\ 654} = 3.5$, $P = 0.062$) and the FCM response increased with outside temperature (range 1.8–9.9 °C) on the sampling day ($F_{1,\ 554} = 5.4$, $P = 0.020$).

3.4. Behaviour baseline and response to relocation to a novel cage

The behaviour observed on days −1, 5 and 10 relative to relocation to a novel cage was coherent to the group they were selected for (Table 3). Exceptions occurred for two out of the 150 mink. One PACERS mink did pace in six out of ten original observation rounds; likewise pacing was her only type of SB (28% of time spent) on day −1. However, after relocation, this mink increasingly performed stationary SB (4% day 5, 23% day 10), and reduced pacing (26% day 5, 3% day 10) plus fur-chewing (day 0: 0.5 cm) on her tail. Therefore, we allocated this mink to group MIXED for the rest of the study to avoid misclassification. One ORALSB mink, originally performing oral SB in two out of ten observation rounds, was not seen performing this SB again (days −1, 5, and 10), but performed pacing (day 5: 9%, day 10: 5%) and stationary SB (day 10 only: 3%). This mink is included in the results (Table 3-7) but discarded from the pools of animals selected to enter the RW part of the study.

Table 3
Location and behaviour of mink (n=150) before and after relocation to a novel cage pooled for days −1, 5 and 10. SB: Stereotypical behaviour.

	In nest box	Passive	Active	Licking SB[1]	Stationary SB	Pacing SB
NONE	63 ±13.5^a	62 ±3.5^a	33 ±3.1^a	0 ±0.2^a	1 ±0.4^a	3 ±1.0^a
FURCHEW	71 ±4.7^a	73 ±4.3^a	26 ±3.9^a	0^a	0 ±0.4^a	1 ±0.7^a
ORALSB	36 ±5.0^b	36 ±5.0^b	37 ±4.3^a	26 ±5.0^b	1 ±0.3^a	1 ±0.6^a
STATSB	10 ±2.6^c	11 ±2.9^c	52 ±3.3^b	0 ±0.0^a	32 ±3.0^b	4 ±1.0^b
PACERS	9 ±1.8^c	11 ±1.8^c	55 ±2.4^b	0^a	1 ±0.4^a	33 ±2.5^c
MIXED	16 ±3.1^c	18 ±3.2^c	46 ±3.3^b	1 ±0.6^b	9 ±1.9^c	26 ±3.5^d
Test value	$F_{5,145}$=42.4	$F_{5,145}$=41.2	$F_{5,146}$=8.0	$F_{10,288}$ =5.3[1]	$F_{5,145}$=53.1	$F_{5,146}$=50.3
P-value	< 0.001	<0.001	<0.001	< 0.001	<0.001	<0.001

Location and behaviour as mean ±SE proportion of observation time, %. Behaviour categories (passive, active, licking SB, stationary SB and Pacing SB) were mutually exclusive, i.e. sum up to 100% per mink. For the location, if not in the nest box, then in the wire cage.

^{abcd}Different letters within columns indicate a significant difference between groups, $P \leq 0.05$. [1]Group and test day interaction, see text for details.

Results for behaviour in Table 3 are pooled for days −1, 5, and 10 relative to the relocation to a novel cage, as the interaction between the group and days was insignificant for all variables, except for licking SB ($F_{10,288} = 5.3$, $P < 0.001$). The time spent in licking SB declined for group ORALSB mink only ($F_{2,\ 32} = 3.5$, $P = 0.042$; Licking SB, percentage day −1: 37^a, day 5: 26^{ab}, day 10: 14^b); licking SB was consistently absent or very rare to observe in the other groups of mink (Table 3).

The groups differed in the proportion of time spent in the nest box. NONE and FURCHEW mink spent about twice the amount of time in the nest box compared to ORALSB mink. ORALSB mink spent about two to four more time than the STATSB, PACERS, and MIXED mink; the latter three groups staying the shortest proportion of observation time in the nest box (Table 3). There was a general effect of observation day ($F_{2,\ 298} = 9.7$, $P < 0.001$), as the time spent in the nest box was longer on day 10 (43 ±3.4%^{a}) than day −1 (31 ±3.1%^{b}) and day 5 (29 ±3.5%^{b}). Further, the mink were more inside the nest box ($F_{1,\ 298} = 9.5$, $P = 0.004$) and thus more passive ($F_{1,\ 293} = 11.2$, $P < 0.001$) with decreasing outdoor temperatures (Table 3). Likewise for the day effect ($F_{2,\ 298} = 8.5$, $P < 0.001$), mink were more passive on day 10 (44 ±2.8%^{a}) than days 5 (28 ±2.9%^{b}) and day −1 (33 ±2.4%^{b}) relative to the relocation. Overall, activity out in the cage was higher in groups STATSB, PACERS, and MIXED mink (46–55%) than in groups NONE, FURCHEW, and ORALSB mink (26–37%; Table 3). There was a general day effect on normal behavioural activity ($F_{2,\ 299} = 8.7$, $P < 0.001$; day −1: 47 ±2.4%^{a}, day 5: 42 ±2.8%^{ab}, day 10: 35 ±2.7%^{b}), and mink were less active with decreasing outer temperatures ($F_{1,\ 304} = 5.9$, $P = 0.016$).

In contrast to normal behaviour (active out in the cage) and staying in the nest box, the duration of the behaviours defined as abnormal (licking, stationary, and pacing SB) were unaffected by the outer temperature. The amount of pacing differed between observation days ($F_{2,\ 298} = 11.4$, $P < 0.00$), with a higher occurrence on day 5 after relocation to the novel cage (day −1: 8 ±1.4%^{a}, day 5: 16 ±1.4%^{b}, day 10: ±11 1.4^a).

The incidence of scrabble events was low, with 26 mink on day −1, 10 mink on day 5, and 18 mink on day 10 displaying at least one scratching on the cage/inventory by one or both front paws; none met the uninterrupted repetitions criteria of three times to qualify as SB. The front paw scratching was more prevalent in groups ORALSB and MIXED before relocation (day −1: $F_{5,\ 144} = 3.1$, $P = 0.010$; NONE: 0 ±0.2^a, FURCHEW: 0^{ab}, ORALSB: 7 ±3.0^b, STATSB: 0 ±0.3^{ac}, PACERS: 0 ±0.3^a, MIXED: 3 ±1.9^{bc}). This group difference in pawing did not persist during consecutive days of observations after relocation to a novel cage (Day 5: $F_{5,\ 144} = 1.5$, $P = 0.21$; all groups: 1 ±0.2; Day 10: $F_{5,\ 144} = 1.6$, $P = 0.17$; all groups: 1 ±0.2). Biting directed to the wire (non-stereotypic) was rarely observed, in total recorded 22 times across all groups over the three observation days (Day −1: 9 mink, Day 5: 5 mink, and Day 10: 8 mink), and thus not analysed statistically. Screams did not occur during the observations.

Signs of fur-chewing were measured on the day of relocation (day 0), while the mink was in the transport cage. Although all NONE mink originally were free from fur-chewing, two out of the 35 NONE mink (5.7%) had 1 cm of fur damage on the tail tip on the relocation day 0. Additionally, three out of 17 ORALSB mink (17.6%; 1, 1.5, and 2 cm), two out of 22 STATSB mink (9.1%; 0.2, and 1 cm), and three out of 33 PACERS mink (9.1%; 0.5, 0.5, and 1 cm) had signs of fur-chewing on the tail tip. Groups still differed markedly in the amount of fur-chewing ($F_{5,\ 144} = 33.9$, $P < 0.001$), being higher in FURCHEW than in MIXED, and both groups being more affected than the other groups (cm tail-chewing, NONE: 0.1 ±0.02^a, FURCHEW: 2.8 ±0.24^b, ORALSB: 0.3 ±0.08^a, STATSB 0.1 ±0.03^a, PACERS: 0.1 ±0.02^a, MIXED: 2.2 ±0.24^c).

3.5. Running wheel activity

The groups differed in running wheel activity measured as revolutions per day, rpd ($F_{5,\ 131} = 10.0$, $P < 0.001$). There was no group difference in the development of running wheel (RW) activity over days (Group and day interaction: $F_{5,\ 164} = 0.31$, $P = 0.91$), but a tendency for a weak increase in running activity over the days 0–10 ($F_{1,\ 168} = 3.0$, $P = 0.086$; Fig. 3). NONE mink ran less per day (rpd: 344 ± 35.3a, N=18) than STATSB (1445 ± 96.1c, N=15), PACERS (1435 ± 118.1bc, N=17) and MIXED (1929 ± 153.1c, N=13) mink, but not significantly different from FURCHEW (485 ± 55.8a, N=14) and ORALSB (466 ± 45.5 ab, N= 11) mink. This wheel activity corresponds to an average daily 'travel distance' of 408–575 m in NONE, FURCHEW, and ORALSB mink, 1.6–1.7 km in PACERS, STATSB mink, and 2.3 km in MIXED mink females, based on the number of revolutions of the wheel with a perimeter of 118.5 cm. The maximum distance was 10.4 km (8811 revolutions per

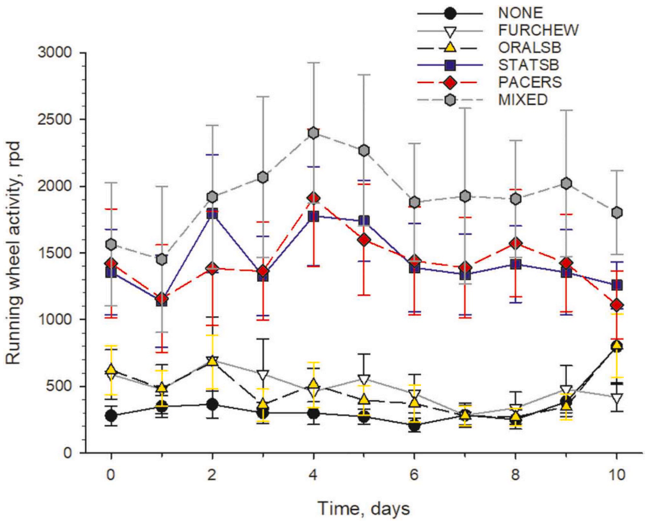

Fig. 3. Running wheel activity in mink from the six experimental groups, as mean ±se revolutions per day, rpd. The groups differed in running wheel activity (P < 0.001), and the mink used the running wheels continuously, see text for details.

24 h) by one MIXED mink on day 7 of running wheel access. The majority of mink (94.3%) activated the RW revolution counter every day; five out of 88 (5.7%) mink did not: two from NONE and one from PACERS on day 0, one FURCHEW on day 9, and one FURCHEW mink on days 2–7 and 9–10.

3.6. *FCMs in response to running wheel access for 10 days*

The concentration of cortisol metabolites (FCMs; supplementary information S8) was on average 39% higher when mink no longer had access (day 15–20: mean ±SE: 455 ± 64.1 ng/g) than during the period with free access to running wheels (day 5–10: 327 ±65.5 ng/g; $F_{1,\,246} = 7.5$, $P = 0.007$). There was no interaction between the group and period ($F_{5,\,237} = 1.0$, $P = 0.44$), and the groups did not differ significantly in FCMs ($F_{5,\,79.2} = 0.4$, $P = 0.86$). The mean FCM level before relocation to cages with running wheel access – included as an individual baseline covariate in the statistical analysis – was 419 ± 65.5 ng/g (day −1). The concentration of FCMs declined slightly with increasing sampling hour ($F_{1,\,311} = 20.6$, $P < 0.001$; range: h 10–17) and with the outside temperature ($F_{1,\,251} = 5.9$, $P = 0.002$; range: 1.1–9.9 °C) during the sampling days. The measured concentration of FCMs ranged from 18 to 7595 ng/g in mink faeces; this high variation and the relatively low number of replications (cf. supplementary information S8) rendered it difficult to detect group differences in the present study.

3.7. *Abnormal behaviour in response to running wheel access for 10 days*

Behaviour was analysed for three periods, before (day −1), during (days 5 and 10) and after (post-RW day +5 and +10) the ten days with access to a running wheel. The performance of licking SB was analysed statistically for groups ORALSB and MIXED only, due to rare incidences in the other groups. Licking SB was not significantly reduced during running wheel access; however, it increased in group ORALSB and MIXED when the mink were returned to a standard cage without a running wheel (Table 4). The performance of stationary SB was analysed for groups STATSB, and MIXED, and this abnormal behaviour was during running wheel access reduced to approximately one-third or less of the time spent in periods before and after running wheel access (Table 4). The performance of pacing was analysed for groups STATSB, PACERS, and MIXED. There was a tendency ($P = 0.086$) for reducing pacing duration during RW access in STATSB, performing pacing at a low level (Table 4). For group PACERS, running wheel access more than halved the time spent in pacing. Furthermore, the duration of pacing increased to an even higher duration after relocation to a standard cage without running wheel possibility. In group MIXED, wheels reduced pacing markedly (from 17% to 4%), with the pacing activity restored to pre-RW level in the period after RW access (Table 4).

There was no interaction between the group and RW period for the duration of both stay in the nest box ($F_{10,\,163} = 1.3$, $P = 0.22$) and the activity of normal behaviour out in the cage ($F_{10,\,159} = 1.1$, $P = 0.39$). The mink were more in the nest box during the period with RW access ($F_{2,\,124} = 6.6$, $P = 0.002$; Before: 39 ± 4.5%^{a}, During: 49 ± 3.0%^{b}, After: 35 ± 3.1%^{a}), with some differences between groups ($F_{5,\,155} = 59.0$, $P < 0.001$) across periods; mink in groups NONE and FURCHEW spent the majority of their time in the nest box, followed by groups ORALSB, MIXED, STATSB and PACERS mink, using much less time inside the nest box (NONE 79 ± 3.3%^{a}, FURCHEW 75 ± 3.9%^{a}, ORALSB 44 ± 5.6%^{b}, STATSB 15 ± 3.0%^{cd}, PACERS 10 ± 2.1%^{c}, MIXED 25 ± 4.4%^{d}). The normal behavioural activity out in the cage – running wheel activity not included – tended to be higher during than after RW access ($F_{2,\,122} = 2.6$, $P = 0.078$; Before: 37 ± 3.1%, During: 39 ± 2.7%, After: 32 ± 2.0%). Groups differed in normal behavioural activity ($F_{5,\,142} = 20.6$, $P < 0.001$), i.e. activity out in the cage not being in the running wheel or abnormal; this activity was higher in groups STATSB (54 ± 3.2%^{a}), PACERS (51 ± 2.6%^{a}), and MIXED (45 ± 3.8%^{a}) than in groups FURCHEW (22 ± 3.5%^{b}), ORALSB (19 ± 3.3%^{b}), and NONE (19 ± 2.9%^{b}).

Scrabbling appeared more prevalent in ORALSB mink, with 9/11 mink displaying this behaviour at least once at some point (prevalence in other groups: 4/18 in NONE, 4/14 in FURCHEW, 4/15 in STATSB, 3/18 in PACERS, 3/12 in MIXED). However, across groups, the median [25%; 75% quartile] of scrabbling was 0 [0; 0]. Consequently, statistical analysis was feasible for three groups only, with no change in scrabble counts before vs during vs after RW access (ORALSB: $F_{2,\,22} = 1.6$, $P = 0.22$; PACERS: $F_{2,\,36} = 0.2$, $P = 0.79$; MIXED: $F_{2,\,24} = 0.4$, $P = 0.68$). The occurrence of bites was low (median 0 [0; 0]), with statistical analysis feasible for group ORALSB only (NS difference between periods; $F_{2,\,22} = 0.3$, $P = 0.74$; observed in 4/11 mink). In the other groups, few mink (in total 11 out of 77) bit the wire at least once at some point during the five days of observation.

4. Discussion

We hypothesised that animals without abnormal behaviour would be (1) more explorative, less fearful plus have lower baseline and response levels of FCMs, (2) better learners, and (3) less behaviourally influenced

Table 4
The proportion of time spent in three types of stereotypic behaviour (SB) – licking, stationary and pacing SB – in mink (n=88) before, during, and after access to running wheel.

	Group	Before	During	After	Test statistics	P-value
Licking SB	NONE	0	0	2 ±2.2	NA	-
	FURCHEW	0	0	0	NA	-
	ORALSB	22 ±10.2^{a}	24 ±6.7^{a}	56 ±8.3^{b}	$F_{2,13.6}$=4.2	0.037
	STATSB	0	0	0	NA	-
	PACERS	0	0	1 ±0.9	NA	-
	MIXED	2 ±2.3^{a}	0^{a}	7 ±4.7^{b}	$F_{2,47.3}$=6.1	0.004
Stationary SB	NONE	0	0	0 ±0.2	NA	-
	FURCHEW	0	0	1 ±1.0	NA	-
	ORALSB	0 ±0.3	0 ±0.0	1 ±0.7	NA	-
	STATSB	36 ±6.2^{a}	12 ±3.9^{b}	37 ±4.0^{a}	$F_{2,58}$=15.0	<0.001
	PACERS	3 ±1.7	1 ±0.8	1 ±0.4	NA	-
	MIXED	21 ±6.9^{a}	8 ±3.6^{b}	21 ±4.8^{a}	$F_{2,46}$=7.9	0.001
Pacing	NONE	0	1 ±0.8	3 ±1.4	NA	-
	FURCHEW	1 ±0.5	1 ±0.9	1 ±0.7	NA	-
	ORALSB	1 ±0.8	0	0	NA	-
	STATSB	3 ±3.1	1 ±1.1	3 ±1.4	$F_{2,65.4}$=2.6	0.086
	PACERS	38 ±5.0^{a}	17 ±4.4^{b}	55 ±2.7^{c}	$F_{2,21.2}$=21.2	<0.001
	MIXED	17 ±8.8^{a}	4 ±2.9^{b}	15 ±5.2^{a}	$F_{2,44.3}$=5.7	0.007

Results are given as mean ± se % of observation time the day before (−1), during (days 5, 10), and after (days 15, 20) 10 days with access to a running wheel.
^{abc}Different letters within rows indicate a significant difference between periods, $P \leq 0.05$. NA: Not available, too few observations for statistical analysis.

by periodic access to running wheels for enrichment. Further, we explored whether groups of mink with different forms of abnormal behaviour differed in these three domains, i.e. in their fear and stress responses, learning performance and use of the wheel enrichment. These results on the heterogeneity of abnormal behaviour contribute to the discussion of whether all forms are equally associated with reduced welfare.

4.1. *Fear and stress response: more investigative sniffing in mink without abnormal behaviour*

4.1.1. *The temperament test*

The temperament test has previously demonstrated its capacity to reflect generalised traits of exploration and fearfulness in farm mink (Malmkvist and Hansen, 2002), states associated with animal welfare. A version of the temperament test has since 2017 been included in the welfare assessment on mink farms in Europe (Henriksen et al., 2022), with the proportion of mink scored 'fearful' reducing the welfare score calculated for each farm in the WelFur programme. The proportion of mink with abnormal behaviour is also reducing the welfare score (Møller et al., 2015). An association between temperament and abnormal behaviour is, however, not always obvious as mink selected for and against stereotypic behaviour over generations did not differ significantly in their temperament (Svendsen et al., 2013).

In our study, NONE mink were more explorative than mink with abnormal behaviour. Specifically, mink with stereotypic and/or fur-chewing behaviour spent a shorter time in investigative sniffing toward the stimulus – a human-held wooden tongue spatula – during the test. This finding fits well with our expectations of signs of better welfare in the NONE mink. Supporting those expectations of coherence across indicators of welfare, the addition of cage enrichments (e.g. shelf, tube, biting ropes, chain and balls) was found to both reduce the occurrence of abnormal behaviour (Hansen et al., 2007; Meagher et al., 2014) and induce a shift towards less avoidance (Meagher et al., 2014) plus more voluntary approach and exploration (Bak and Malmkvist, 2020) in farm mink in the temperament test.

The mink in our study generally responded with low fearfulness, indicated by a low incidence of active avoidance (2%) during the test. The proportion of aggressive mink (29%) appeared high compared to the range of 0–14% in previous studies (Hansen and Møller, 2001; Malmkvist and Hansen, 2002; Hansen et al., 2011; Bak and Malmkvist, 2020), however, based on juveniles and not adult females as in the present study.

A higher proportion of mink in groups NONE and ORALSB was categorised as 'explorative' in comparison to groups FURCHEW and PACER; although the measured duration spent in explorative interaction was higher for NONE mink only. The higher proportion of mink with stereotypic licking categorised as 'explorative' by the assessor – blinded concerning group allocation – was unexpected. To our knowledge, this is the first study to test oral stereotypies in mink. In a strain of laboratory mice, a positive association between adult stereotypic wire-gnawing and exploratory behaviour was suggested (Wurbel and Stauffacher 1997). Likewise, the performance of oral stereotypies in horses ('crib-biting') was linked with lower levels of a PCA factor termed 'Anxiety', although based on answers from horse owners rather than on direct observations of the animals (Nagy et al., 2010). However, we cannot exclude that the temperament score of ORALSB mink is an artefact of their initial position during the temperament test. Mink standing close to the cage opening – as during most repetitive wire-licking (pers. observation, cf. video supplementary information S1) – only have a few cm to move to engage in sniffing the test spatula; this bias to front cage locations may push the temperament score towards 'explorative' in the test. This explanation is supported by results showing that the initial position of mink close to the front lid – induced by placement of a resting shelf in the front rather than in the back of the cage – led to a higher proportion of mink being scored into the explorative category in the temperament test (Henriksen et al., 2020). Further, ORALSB mink lost interest in exploration after a significantly shorter duration than NONE mink. In that respect, ORALSB reacted equally to the groups of mink with other forms of abnormal behaviour, which all spent significantly less time in exploratory behaviour directed to the test stimulus than did NONE mink.

4.1.2. *Hypothalamic-Pituitary-Adrenal (HPA)-axis activity*

The results on HPA-axis activity – measured as faecal cortisol metabolites (FCMs) during baseline conditions and in response to handling/transfer to a novel cage – were inconclusive. We expected NONE mink to be characterised by a lower baseline and response FCM levels than mink with abnormal behaviour, and wished to compare HPA-activity in mink displaying the different forms of abnormal behaviour. However, we failed to demonstrate a difference in FCM baseline and responses in our study with 17–35 mink per group. A previous study, reporting higher baseline and response FCMs in stereotypic (SB) versus in non-stereotypic mink, was based on a higher number of mink (80−81) per group; the baseline FCM concentration was reported to be 79 ng/g for SB and 51 ng/g for non-SB mink (Malmkvist et al., 2011). In the present study, we report 4–6 times higher baseline means (314 ng/g for mink with abnormal behaviour, 293 ng/g for NONE mink), using the same sampling methodology. We cannot exclude that a high baseline concentration may blur responses to an additional stressor due to a ceiling effect (Mormede et al., 2007). Additionally, the standard deviation exceeded the mean value of FCMs in all six experimental groups. The relative variation, CV (= SD/mean), averaged 175% in abnormal and 163% in NONE mink, whereas CV was 85% in SB and 64% in non-SB mink previously studied in (Malmkvist et al., 2011), both studies on adult female mink at the same research farm. We conclude that high variation renders FCM data from the present study infeasible for determining baseline and response differences between the six experimental groups.

4.2. *Mink with some forms of abnormal behaviour passed more stages in the learning test*

Mink with some forms of stereotypic behaviour (groups PACERS, MIXED) outperformed both NONE and ORALSB mink in overall performance in the learning task. Thus, mink with primarily locomotory forms of SB passed more of the three learning stages. Although this finding was unexpected according to our hypothesis, it may be in line with previous findings of a positive association between stereotypies and novel cell formation in parts of the brain involved in learning and memory; hippocampal neurogenesis increased in mink with the performance of stereotypic behaviour (Malmkvist et al., 2012), predominantly of the pacing form. The authors suggested that the increased motor activity in mink with certain forms of abnormal behaviour – such as pacing – might account for the positive effect on hippocampal cell proliferation, in comparison to less active mink held under the same conditions (Malmkvist et al., 2012). Likewise, other studies demonstrated that exercise (voluntary wheel running) enhances neurogenesis in the hippocampus of adult laboratory mice (van Praag et al., 1999). Conversely, a low formation of novel cells and cell death in the hippocampus is a consequence of prolonged stress and ageing in mammals (Lupien et al., 1998), concurrent with impaired learning and memory function.

Previous studies in adult female mink reported a positive correlation between locomotor SB and so-called recurring perseveration (Dallaire et al., 2011), i.e. the tendency for animals to repeat a response regardless of the absence of relevant stimuli. However, this finding was not replicated in male mink – housed under enriched or non-enriched conditions that influence the occurrence of SB – using the same test setup (Campbell et al., 2013). The authors clarified that feeding motivation could explain some of the outcomes from the test of perseverance, as the active SB mink acquired more rewards during the test, a two-choice situation with a 50% reward chance at random (Campbell et al., 2013). Thus, the mink response may depend on hunger and reward sensitivity rather than reflecting a continued response to an irrelevant stimulus only. We used a different testing approach addressing learning performance, with one of two simultaneously presented stimuli rewarded upon the correct choice and one punished upon incorrect choice, until the mink faced a shift in stimulus assignment during the reversal stage. The experimental groups did not differ in their proportion of rewarded trials, thus differences in feeding motivation did not appear to be a confounder for the results on learning performance in our study. In case perseveration was higher in SB mink, we would predict that they performed less well in the reversal stage of the learning test; this did not appear to be the case, although the comparison of abnormal to NONE mink is hampered by the fact that only 1 out of 7 NONE mink passed the reversal stage (equal to 14%). However, the number of mink ready for the reversal stage (7 NONE and 12–18 of abnormal mink per group) is within the range of group sizes used in previous studies of associations between stereotypic behaviour and performance in two-choice tasks for farm mink [n=5–14 in Dallaire et al. (2011), n=13–15 in Campbell et al. (2013)]. Nearly half of the mink with abnormal behaviour (46%, 24 out of 52 mink) – reached the reversal stage, of which 33% passed successfully. Thus, we provide no evidence for increased perseverance among mink with abnormal behaviour of different forms, i.e. they did not keep responding to a stimulus that was no longer rewarded.

We used a reversal task. It should be noted that responses in reversal vs. extinction tasks may not reflect the same type of learning. Several studies demonstrated enhanced resistance to extinction in stereotypic individuals, e.g. dogs (Protopopova et al., 2014) and horses (Hemmings et al., 2007). However, oral SB horses responded with more lever presses for food also in the acquisition phases (Hemmings et al., 2007), which may indicate a higher motivation for performing the task, e.g. due to hunger or a higher reward sensitivity. Highly palatable rewards are potent inducers of cribbing behaviour in horses, possibly mediated through the opioid and dopaminergic systems (Albright et al., 2017). In another study, oral SB horses performed as control horses during a visual reversal learning test (Freymond et al., 2019). In our study, SB animals were not persistent in responding to the previously rewarded cue. Thereby our study supplements the previous findings of associations between learning and abnormal behaviour.

In the present study – as true for the majority of studies on groups of animals with and without abnormal behaviour – we report associations. Thus, we cannot determine whether the reported difference is induced by abnormal behaviour or concurrent responses modulated by individual variation in e.g. sensitivity and the predisposition for developing stereotypies [also discussed in Ijichi et al. (2013)]. For example, we cannot exclude that farm mink with higher cognitive abilities/learning skills are more prone to developing abnormal behaviour in the relatively barren housing environment; if so, 'clever' mink may be over-represented in the abnormal groups, and then account for the better learning performance observed. This hypothesis could be tested in future studies of mechanisms behind the positive associations between learning performance and some forms of abnormal behaviour. However, the lower learning performance in mink with licking stereotypies suggests that this hypothesis cannot be true for all forms of abnormal behaviour. Further, we speculate that activity (both abnormal and normal) are more predominant in pacing than in passive mink (e.g. in groups NONE and ORALSB), thereby favouring their learning performance by an activity-induced improved hippocampus function in active individuals, as previously discussed.

4.3. Stereotypic mink, except for with licking form, ran more in wheels

Regarding the use of the running wheel, an acclimation period is suggested for rodents to accomplish a plateau of running (Novak et al., 2012) – however, this was not obvious in the adult mink over the 10-day study period. Most of the mink (97%) ran in the running wheel within the first day of access (mean: 1000 rpd), with no significant development over the study period. A previous study (Hansen and Damgaard, 2009) reported females 'travelling' up to 13 km per 24 h for stereotypic mink. In comparison, the maximum running distance measured in our study was 10.4 km per 24 h by one mink from group MIXED. The daily average wheel revolutions were roughly 3–5 times larger in mink from groups PACERS, STATSB and MIXED than for mink in groups NONE, FURCHEW and ORALSB.

Behind this result lies that wheel running is rewarding and caged farm mink will lever-press for access to running wheels (Hansen and Jensen, 2006). In nature, both wild and feral mink patrol within a home range to forage and scan for intruders and partners. American mink may travel several km daily, and the distance covered depends on the reproductive condition, competition, season, food abundance (Halbrook and Petach, 2018), sex, and predation risk (Salo et al., 2010). Farm mink engage in more wheel-running before feeding and particularly under periods of feed restriction; the activity peaks at dawn and dusk is believed to reflect an adaptive synchronization of foraging behaviour in mink with the activity pattern of their prey (Zielinski, 1986).

NONE mink ran markedly less than PACERS, STATSB, and MIXED, but not significantly different from FURCHEW and ORALSB mink. Likewise, one previous study of wheel-use in mink (Hansen and Damgaard, 2009) found that mink with SB (unspecified forms) ran more than non-SB mink upon periodical wheel access. We were interested to learn whether e.g. mink with stationary SB – one class sometimes differentiated from pacing in studies of farm mink – behaved differently, but this was not the case. All forms of SB, except stereotypical licking, were reduced in mink during the period of wheel access. This result underlines that oral stereotypies appear of a different nature than the other forms of stereotypies.

The reasons some SB mink use the wheel more could be due to increased reward-seeking or the amount of reward experienced by the animal from wheel running; involving e.g. dopaminergic modulation and endogenous opioids [reviewed in Novak et al. (2012)].

4.4. Non-responders

In animal studies reporting trained responses, researchers may exclude a proportion of the animals failing to meet certain learning criteria or appearing uncooperative. In our study, we had to give up on 2 out of 91 mink recruited for the learning task. These two mink took no or few rewards before they retracted into their nest box. Further, we cannot exclude that we could have recruited more mink for the reversal stage of the learning task if we had continued with the training for longer than five consecutive days – however, we have no data on this. Non-responders exist across studies, e.g. 22.2% of the assigned mink were unable to meet the training criteria of the perseveration test used by Campbell et al. (2013). We consider that non-responders potentially may introduce a bias in ethological studies on learning and cognitive performance. The proportion of mink failing to enter the learning task was low (2.2%) in our study, and comparable to the proportion of 2.7% non-responders in a spatial learning study of domestic horses (Freymond et al., 2020).

4.5. Stability of behavioural groups

The type of abnormal behaviour in the different groups was consistent throughout the observation period, including across the cage relocation. Overall, 148 out of the 150 mink (98.7%), kept their behavioural phenotype, whereas two mink made an obvious shift; one changed its prevalent type of SB from pacing to a stationary form, and one mink with a low amount of stereotypic licking stopped during the observation period. The relocation induced a transiently elevated level of pacing, which we interpret as a stress response to the cage shift, although we did not include a group of unmoved mink for comparison. Other studies have found increased SB in response to stressors induced by management around weaning (Malmkvist et al., 2016), feeding (Malmkvist et al., 2013), and housing (Hansen et al., 2007; Meagher et al., 2014).

Experimental investigation of the specific factors that predispose and release different forms of abnormal behaviour may help in our understanding of the nature behind specific forms. Further, a proportion of the mink displayed several forms, typically as a mix of pacing, stationary, licking forms of SB with signs of fur-chewing on the tail. These 'abnormal generalists' were included in the group MIXED of our study. Self-inflicted fur-chewing, i.e. oral hair removal typically on the tail, is an abnormal behaviour in mink, with an increase observed after stressors such as early weaning (Mason, 1994) and housing juveniles alone (rather than in pairs) and in adult females after removal of their kits at weaning separation (Hansen et al., 1998). Fur-chewing can be reduced during improved management such as cage enrichment (Meagher et al., 2014) and access to biting ropes or chunky feed (Malmkvist et al., 2013). The challenge of fur-chewing is that this behaviour is hard to observe directly; instead, indirect evidence is used by measuring the area of the animal, affected by pelage damage. Therefore, we cannot exclude that milder forms of tail-suckling or not hair-damaging forms are overlooked. During the study time (from October to December), an increasing number of mink showed signs of fur-chewing on the tail; ten out of 107 the mink outside the FURCHEW and MIXED groups developed milder signs of fur-chewing on the tail. This increase is in accordance with previous findings of the number of mink with fur-chewing on the tail increasing in adult mink from December to February (Hansen et al., 1998) and may be related to environmental changes as also suggested for self-grooming in other species (Luo et al., 2023). Another point to consider is the yearly pelt changes, with the change from summer to winter pelt – running from the tail towards the head – in the first weeks of October (Blomstedt, 1989). Thus, the manifestation of fur-chewing behaviour can be less visible in mink during the early part of the observation period. Still, the FURCHEW and MIXED mink were markedly more affected by fur-chewing, on average 2–3 cm of the tail equivalent to 7–28 times higher propagation of affected area than in the other groups.

Initially, we aimed to create a group of mink performing stereotypical front-leg scrabbling [cf. Diez-Leon et al. (2019)], however, this failed as the behaviour gradually became less repeated and reduced in occurrence as the direct observations progressed. We suggest further studies of whether scrabbling in mink may be modulated by the presence of a human observer. In contrast, for the other forms of abnormal behaviour, we report evidence for relatively high stability and persistence over time. We present results from the 'solid' performers selected for our distinct experimental groups, which may not be representative of the average farm mink population. Further studies can investigate whether farm mink with less intense or clear patterns of abnormal behaviour may be equally consistent or rather more able to shift between the different forms.

4.6. *Conclusion*

We included a group of animals, which were apparently free from abnormal behaviour, as a reference group in the present study. These NONE mink were generally less active out in the cage, however, they spent more time in investigative sniffing than mink with abnormal behaviour during a temperament test. We failed to confirm reduced HPA-axis activity in NONE mink; large individual variation in faecal cortisol metabolites (FCMs) rendered this indicator insensitive to detect group differences. Abnormal behaviour was not associated with impaired learning; rather, mink with locomotory forms of SB outperformed NONE mink (and mink with licking SB) in the learning test, suggesting a link between activity and learning. Mink with an SB involving locomotion and/or up-down movements used running wheels extensively, whereas NONE mink and mink with other forms of abnormal behaviour (ORALSB, FURCHEW) exercised less. All forms of stereotypies, except licking, were markedly reduced during wheel access. Oral stereotypies appear to be of a different nature than the other forms of stereotypies. The current study underlines that running wheels constitute an enrichment that is valued by farmed mink. Further, based on the results, we should consider that low activity and performing repetitive licking represent welfare challenges rather than focusing on the highly active individuals only. In conclusion, different forms of abnormal behaviour appear associated with different cognitive and motivational characteristics as demonstrated in farm mink.

CRediT authorship contribution statement

Malmkvist Jens: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing. **Díez-León María:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Christensen Janne Winther:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Danish Pelt Levy Foundation (2019) for funding this project. The funding sources had no involvement in the study design, data collection, analysis, interpretation or other part of the preparation and submission of the paper. Professor Rupert Palme, Department of Biomedical Sciences, University of Veterinary Medicine Vienna, Austria, kindly provided us with antibodies for the mink FCM analysis and commented on FCM parts of the material and method section of this manuscript. Dr Torben Larsen was responsible for the FCM analysis at the laboratory at Dept. Animal and Veterinary Sciences, Aarhus University (AU). We additionally thank the staff at the AU Research farm, plus the AU technicians Birthe Houbak, Carsten K. Christensen, Dines T. Bolt, Mads R. Jensen and AU student Agnete Gargulak for valuable assistance in making the data collection possible.

Research data

Data (six files: 1. ExperimentalMinkGroup.xlsx, 2. TemperamentTest.xlsx, 3. LearningTest.xlsx, 4. BehaviourRelocation.xlsx, 5. FCMBaselineResponse.xlsx, and 6. RunningWheelActivity.xlsx) are available at the repository: https://www.erda.au.dk/archives/522934ad85cf9289937cdeb331a6658b/published-archive.html.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2024.106167.

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