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Effects of enrichment on boredom-like states in mink and their behavioural correlates: a replicate study

Rebecca K. Meagher[1*], Dana L.M. Campbell[2], Georgia J. Mason
University of Guelph, 50 Stone Rd. E., Guelph, ON, CANADA, N1G 2W1
[1] Present address: School of Agriculture, Policy & Development, University of Reading
Whiteknights, PO Box 237, Reading, Berkshire, UK, RG6 6AR
rkmeagher@gmail.com
*corresponding author
[2] Present address: CSIRO, Agriculture and Food, Armidale, NSW 2350, Australia

Abstract

Scientists and laypeople have long expressed concern that animals in non-enriched, unchanging environments might experience boredom. However, this had attracted little empirical study: the state is difficult to assess without verbal self-reports, and spontaneous behavioural signs of boredom can vary in humans, making it hard to identify signs likely to be valid in other species. We operationally define boredom as a negative state that causes an increased, generalised interest in diverse stimuli. Previously, we demonstrated that this state existed in mink housed in non-enriched cages, compared to those in preferred, stress-reducing enriched enclosures; and that this heightened interest in stimuli positively correlated with time spent lying still but awake, while negatively correlating with locomotor stereotypic behaviour. However, these results needed replication. The current study tested for the same effects, in a new cohort of 20 male mink, by presenting 11 stimuli ranging from those predicted to typically be aversive (e.g. predator cues) to those predicted to be rewarding (e.g. food rewards; moving objects to chase). Where housing treatments differed, non-enriched mink were again more interested in the stimuli presented, spending longer oriented towards and in contact with them (e.g. for aversive stimuli: $F_{1,9}$=6.27, p=0.034 and $F_{1,9}$=8.24, p=0.019, respectively). Lying still but awake again correlated with interest in the stimuli (shorter latencies to contact rewarding stimuli: $F_{1,17}$=3.70, p=0.036; in enriched mink only, more time oriented to and in contact with all stimuli: $F_{1,8}$=9.49, p=0.015 and $F_{1,8}$=15.9, p=0.004). In contrast, the previous correlations with stereotypic behaviour were not replicated. We therefore conclude that mink housed in non-enriched cages likely experience boredom-like states, and that time spent lying still while awake could potentially be used as a cage-side indicator of these states. We also suggest how future researchers might address further fundamental and practical questions about animal boredom, in mink and other species.

Keywords: sensation-seeking; emotional states; Neovison vison; animal welfare; inactivity; environmental enrichment

1. Introduction

Boredom has long been believed to be a widespread problem in captive animals housed in environments that offer little variety or complexity (see e.g. Manteuffel et al., 2009; Wood-Gush and Beilharz, 1983). If true, this would be a major concern for welfare. Boredom is, by definition, aversive, having commonly been defined as a negative subjective state resulting from environments that provide too little stimulation or variety to satisfy psychological needs (e.g.

Berlyne, 1960; Burn, 2017; Kirkden, 2000); see Eastwood et al., 2012 for broader definitions from different theoretical perspectives). Eastwood and colleagues (2012) wrote that "to be bored… is to be in a state of longing for activity but unaware of what it is that one desires and to look to the world to solve the impasse." In humans, prolonged experience of this feeling can be seriously detrimental to well-being: boredom correlates with depression and anxiety (e.g. LePera, 2011; Sommers and Vodanovich, 2000) and even predicts elevated mortality rates (Britton and Shipley, 2010; Maltsberger et al., 2000). It can also motivate risky behaviours such as recreational drug use and perhaps deliberate self-harm, as bored people seek stimulation (Chapman et al., 2006; Samuels and Samuels, 1974; Wiesbeck et al., 1996). Similarly, boredom has sometimes been blamed for problem behaviour in animals, including stereotypic behaviour in many species (Kiley-Worthington, 1977; Wemelsfelder, 1993) and excessive salt-licking in horses (Krzak et al., 1991). However, boredom is difficult to assess in animals because its symptoms in humans are variable, ranging from inactivity to restlessness and stereotypic behaviour (reviewed by Berlyne, 1960; Burn, 2017; Harris, 2000), making it hard to identify spontaneous behaviour patterns that will reliably and validly indicate boredom in diverse species.

An operational definition of boredom is needed in order to validate such possible indicators in non-human animals. We have therefore operationalized boredom as a negative state that (a) is particularly manifest in sub-optimal barren housing (to capture the aversive attributes of this state, and its relation to under-stimulation), and (b) causes hyper-responsiveness to stimuli (to capture the way that enhanced motivation to obtain stimulation should be a defining characteristic) (Meagher and Mason, 2012). Working with American mink, *Neovison vison*, we then compared subjects living in non-enriched housing to mink housed in more complex, variable enriched cages that improved their welfare. We demonstrated that when presented *in situ* with diverse stimuli, ranging from pleasant to mildly aversive or frightening, the non-enriched mink did indeed exhibit more interest in them, generally investigating them faster and for longer (Meagher and Mason, 2012). In this first study, there were also hints of a relationship between this core symptom of a boredom-like state and time spent performing two types of behaviour when undisturbed in the home cage. Time spent lying inactive despite being awake (i.e. inert, but with eyes open) tended to correlate positively with interest in the stimuli presented, identifying this form of inactivity as a potential symptom of boredom. Time spent performing locomotor, head and whole-body stereotypic behaviours (hereafter referred to simply as 'loco' stereotypies following (Diez-Leon et al., 2016) by contrast, tended to correlate negatively with interest in the stimuli, a finding that could cautiously be interpreted as support for the hypothesis that stereotypic behaviour may alleviate boredom (Kiley-Worthington, 1977). However, for both behaviour patterns, the relationships were not consistent across all measures and treatments.

We therefore conducted the current experiment to test whether the previous findings, including these relationships between interest in stimuli and lying still but awake and locomotor stereotypic behaviour, could be replicated. If such behaviours are reliably associated with boredom-like states, these could be very useful indicators for practical welfare assessments (when experimentally assessing animals' responses to multiple probe stimuli, our primary index of boredom, would be highly impractical). The protocol was the same as that for the original experiment, but some of the specific stimuli employed were changed in order to increase the generalisability of the results. Some further differences from the original study likely arose from the fact that this new work was conducted opportunistically at the ‘tail end’ of research on our subjects’ sexual behaviour: an issue we return to in the Discussion.

2. Methods

2.1 Subjects and housing

The subjects were 20 male mink of the Black colour-type (strain): of these, there were nine pairs of brothers, the two siblings of each pair being differentially housed (see below). They had just reached sexual maturity, being 9 to 11 months old during the experimental period. They were housed individually indoors at the Michigan State University research farm (Michigan, USA), in 75 (L) x 60 (W) x 45 (H) cm wire-mesh cages with external wooden nest boxes. These conditions are relatively standard for countries in which enrichment is not required. Mink were fed once per day with a meat-based paste, and had *ad libitum* access to drinking water. The research was approved by the University of Guelph Animal Care Committee, and by Michigan State University’s Institutional Animal Care and Use Committee.

One mink from each sibling pair, the subject randomly allocated to the non-enriched (NE) treatment, was limited to the single cage. The other mink (randomly allocated to the Enriched group; E) were raised and housed with additional access to an enriched compartment of twice the width, reached via a wire mesh “bridge”. This additional cage contained a channel of running water, and new structural or manipulable objects added each month (see Dallaire et al., 2012; Díez-León and Mason, 2016 for more details on these cages). This enrichment treatment had been previously demonstrated to reduce stress and to be valued by mink (Dallaire et al., 2012; Meagher et al., 2013). Enriched and non-enriched cages were evenly distributed throughout the room following a pattern of NE, E, E, NE. All mink had been in their respective housing conditions from the time they were approximately three months of age, with the exception -- for 16 of the 20 males -- of a few hours per day during the mating season (ten days in March during which they were given four to five mating opportunities (as part of a project on sexual behaviour), ending just before we began to present them with beginning of the interest in stimuli as described below. During this mating period, the enriched mink of that group were restricted to their home cages (i.e. to housing identical to that of their non-enriched brothers).

2.2 Spontaneous behaviour

Baseline behaviour was observed through modified instantaneous sampling, as standard for our research group (e.g. as described in Meagher and Mason, 2012). The observations were performed by a single observer over 10 days in December to February, from 8:30 to 14:00 each day; each mink was observed every 15 s for 4 min twice within this period, for a total of 340 observations across all days. Mink were fed at approximately 15:00. As in the previous study, the behaviours of interest were ‘loco’ stereotypy (e.g. pacing or head-twirling; defined as three consecutive repetitions of a movement or series of movements) and lying still but awake (i.e. with the eyes open and visible to the observer). These data were thus collected two to three months prior to our tests for interest in stimuli, but individual differences in mink behaviour are typically very stable, even over far longer time periods than this (Dallaire et al., 2012; Hansen et al., 2010; Mason, 1993).

2.3 Tests for interest in stimuli

A series of 14 behavioural tests per mink were conducted over eight days in late March and early April, after the mating period had ended. The order of these tests and details of the stimuli used are provided in Table 1. Stimuli were categorised *a priori* as likely aversive, likely rewarding, or ambiguous (/neutral) based on their biological / ecological relevance (or lack thereof for ambiguous stimuli). Most stimuli that had appeared to be appropriate representatives of the categories in the original experiment were used again (e.g. the handling glove, as the most clearly aversive based on fear scores, high latency to contact and low time in contact; and the moving brush, as eliciting extremely high levels of interest; Meagher & Mason 2012), while a previous ‘ambiguous’ (neutral) stimulus with the shortest latency to contact (the maraca) was eliminated because it may have been rewarding to the mink. Additional stimuli thought *a priori* to be rewarding based on biological relevance or common usage (pheasant scent as a prey-related cue, and a commercial lure used by trappers to attract mink) were added to improve representation of that category. The predator urine for aversive stimuli (cf. e.g. Apfelbach et al., 2005) was provided by the Detroit Zoo (Royal Oak, Michigan), with urine of two species selected from four available after a brief pilot test on mink not used in the study. All stimuli were equally novel to the mink in both treatments.

Three of the tests measured consumption of food rewards, in which the proportion of treats offered that were consumed within 20 minutes was assessed for all mink simultaneously. The remaining 11 tests assessed investigatory behaviour. In these, a single stimulus was presented to the mink by placing it on top of or in front of the cage for 5 min. After placing the object, the observer (RKM) stepped away from the cage and remained stationary, with the exception of the glove and toothbrush, in which she remained stationary directly in front of the cage with the gloved hand extended (for more details on this protocol, see Meagher et al., 2011). Mink were tested consecutively within rows of cages. These tests alternated between stimuli that had been categorised as aversive, rewarding, or ambiguous. Tests began at 8:30 and 13:30 each day, but no afternoon test was given if an aversive stimulus had been presented in the morning, to allow the mink time to recover. A test only began when the subject mink was in the home compartment; enriched mink were encouraged to return there if necessary by tapping on the cage and/or dragging a cable tie along the top of the cage for a few seconds at a time, but were skipped if they failed to return within 10 min (n=2 over all the 212 tests conducted). If a mink slept for more than 3 min during an attempted test, that animal was skipped and given another opportunity after all other mink had been tested; if they failed to awaken a second time, they were excluded from the analysis for that test (n=11 of the 212 tests).

The latency to make contact with each stimulus, total time in contact with it, and time with the head oriented towards it, with eyes open, were recorded as measures of interest in the stimuli. If the mink never made contact, the maximum latency was assigned. Contact was defined as touching the item with the muzzle or front paws. In addition, as in our previous work, fear was scored live by the presence of four behaviours: retreats (confirmed from video where necessary), alternation between retreat and approach, screams (fear vocalisations), and spraying from the scent glands. Latencies were recorded live, while contact was recorded from video by an observer blind to the hypothesis under test, and orientation was recorded using both methods. Interobserver reliability was therefore checked against live observations for orientation. Unfortunately, the videos were lost before contact time could be assessed by a second observer. Where there were major discrepancies (revealed by outliers in the rank correlation data) for orientation, orientation and contact values for that individual for that test were excluded from the analysis.

2.4 Statistical analysis

To test whether the "aversive" stimuli were in fact more frightening than the others to these mink, we averaged fear scores for each individual within stimulus type, then ran Wilcoxon signed rank tests to compare means for the aversive stimuli to those in each of the other two categories. We also summed fear scores across individuals to examine the pattern across individual stimuli. A Welch's ANOVA was used to compare mean latencies across stimulus types, because variances were unequal.

To assess housing effects on responsiveness to stimuli, the data were analysed using MANOVAs (multivariate analysis of variance) for repeated measures for each dependent variable (latency, orientation, and contact duration and proportion of food treats consumed). These models were run both for all stimuli together, and then, to replicate our previous work, split by stimulus type (rewarding, ambiguous and aversive). Residuals were visually inspected for normality and homogeneity of variance. Latency values were log-transformed for all analyses to correct non-normality of the data. Housing effects on spontaneous behaviour were assessed using a Wilcoxon rank-sum test for lying alert, due to non-normality, and a Welch's ANOVA for locomotor stereotypy, which had unequal variances.

To assess relationships between responsiveness to stimuli and the two spontaneous behaviour patterns of interest, we first obtained least squares means by individual for each dependent variable in general linear models, with individual nested in family as a random factor and stimulus number as a fixed factor (to control for order effects). Latency values were log-transformed to improve normality, as above, and contact duration values were square root-transformed. This approach provided a single index of responsiveness for each measure (latency, orientation, and contact) across all stimuli tested, for each individual mink. These indices could then be regressed against spontaneous behaviour: relationships that were assessed using general linear models, controlling for treatment and its interaction with the behaviour of interest (the interaction term being removed if its p-value was greater than 0.25; Quinn and Keough, 2002).

One-tailed p-values were used because the predictions were directional, since this was a study explicitly trying to replicate previous findings. All analyses were conducted in JMP 12 (SAS Institute Inc., North Carolina, USA).

3. Results

3.1 Validation of stimulus categories

As predicted, latencies differed between stimulus types ($F_{2,32}$=3.79, p=0.033), with rewarding stimuli having the shortest latencies and aversive the longest ones (back-transformed means of least square means, with interquartile ranges: 1.91 s [1.03-3.83 s] vs. 5.06 s [3.83-8.06 s]). Latencies by individual stimulus are presented in Table 1. Similarly, time in contact was highest for rewarding stimuli (back-transformed means: 175 s [IQR: 81-278 s] vs. 87s [21-139 s] and 89 s [38-152 s] and for ambiguous and aversive respectively; Welch's ANOVA $F_{2,36}$=16.0, p<0.001).

Specific indicators of fear were very rarely observed, as is apparent from the summed scores for all individuals in Table 1. Fifteen of twenty mink never exhibited any of these indicators, compared to just 3 of 29 mink or 2 of 14 males in the original experiment (Fisher's p<0.0001 and p=0.001, respectively). Furthermore, only two of the four aversive stimuli, along with the first stimulus presented (which was categorized *a priori* as rewarding), elicited fear behaviour from any individuals. Matched pairs tests did, however, show a tendency for these scores to be higher for aversive than for rewarding or ambiguous stimuli (one-sided p=0.063).

3.2 Housing effects on interest in stimuli

The effects of housing on minks' responses to the stimuli presented are summarised in Table 2 (where they are shown in comparison with the results from the original experiment). In brief, where there were treatment effects here, non-enriched mink again explored the stimuli more than enriched mink did (see Fig. 1). This was true for time in contact, when all stimuli were included in the analysis (contact: $F_{1,4}$=22.8, p=0.004), but for orientation, there was an interaction with test, i.e. the stimulus used ($F_{9.6,48.1}$=2.50, p=0.018; see Table 3 for treatment means by stimulus). Broken down by stimulus type, both of these measures were higher in non-enriched mink for aversive stimuli ($F_{1,8}$=4.12, p=0.038 and $F_{1,8}$=6.97, p=0.015), and there was also a non-significant tendency in this direction for rewarding stimuli (orientation: $F_{1,9}$=4.85, p=0.055; contact: $F_{1,8}$=4.84, p=0.059). For ambiguous stimuli, however, there were further interactions with the individual stimuli for both orientation ($F_{2.8,19.9}$=4.19, p=0.020) and contact ($F_{2.5,17.2}$=4.72, p=0.018), which appeared to be due to responses to a single stimulus, the candle, not being numerically higher in non-enriched mink as they were for the other ambiguous stimuli (see Table 3). There were no treatment effects on latencies to make contact or on food reward consumption, in contrast with the original experiment.

3.3 Behavioural correlates of interest in stimuli

Locomotor stereotypic behaviour was, as expected, reduced by enrichment (mean 0.9% vs. 7.0% of observations, $F_{1,9.5}$=5.39, p=0.044); and 9 of 10 NE mink were seen performing this behaviour vs. 4 of 10 E mink. However, unlike in our original study, time spent lying still but awake was not affected by housing treatment (median 1.0% of observations in NE vs. 0.6% in E, p>0.10; 8 of 10 NE mink performed the behaviour vs. 6 of 10 E mink). Despite this, time spent lying still but awake did show some of the expected relationships with stimulus exploration, as outlined below.

In the analyses with all stimuli, time spent lying still but awake did not correlate with latency to touch. However, for time oriented to all stimuli, there was an interaction with housing treatment (R^2=0.43, $F_{1,16}$=5.47, p=0.033; Fig. 2); and in the enriched treatment only, lying awake correlated positively with time oriented to stimuli ($F_{1,8}$=9.49, p=0.008). The same was true for time in contact with stimuli (R^2=0.53, interaction: $F_{1,19}$=7.54, *p*=0.014; Fig. 3; relationship in enriched mink: $F_{1,8}$=15.9, *p*=0.002).When stimuli were split by sub-type, time spent lying still but awake also correlated negatively with latency to touch, albeit for rewarding stimuli only (R^2=0.22, $F_{1,17}$=3.70, *p*=0.036). In enriched mink, lying awake also correlated positively with time oriented to and in contact with aversive stimuli (orientation: R^2=0.43, $F_{1,8}$=6.06, *p*=0.016; contact: R^2=0.67, $F_{1,8}$=16.6, *p*=0.002) and with contact with ambiguous stimuli (R^2=0.43, $F_{1,8}$=5.95, *p*=0.020). 'Loco' stereotypic behaviour, in contrast, did not correlate with any response to the stimuli overall nor within any category (*p*>0.10). The pattern of results across all measures is summarised in Table 4 (where they are also contrasted with the original study's findings).

4. Discussion

As in our previous work, compared to enriched mink, non-enriched mink showed signs of exaggerated interest in stimuli that were consistent with boredom-like states. There was also some evidence that, as before, the behaviour of lying still despite being awake, was a correlate of this state. Not everything was similar between the original and replicate experiment however: the current mink showed far fewer signs of fear, even when presented with stimuli that should have been threatening; and non-enriched animals now did not spend more time lying awake than enriched ones. The precise patterns of effects across stimulus sub-types also differed (for example, non-enriched mink now did not consume more food treats than enriched mink). In some instances, these differences may have reflected our use of a slightly different set of test stimuli; a degree of uncertainty in both studies in the assignment of stimuli to the rewarding, ambiguous, and aversive categories; and/or low sample sizes for the MANOVAs due to some missing data in the replicate study. However, we also suspect they reflect differences in timing: because the replicate study was conducted just a few days after a 10-day long mating period in which most males, regardless of their rearing and housing conditions, were given regular access to salient positive stimuli (females) and opportunities to perform highly motivated, time-consuming activities (courtship and mating). This could well have reduced boredom and, reduced any difference between housing treatments. We recognise that this timing was non-ideal, but it was unavoidable practically (as we were using a narrow window of opportunity available while facilities and research staff time were available).Despite this, we did successfully replicate the original finding of increased exploratory behaviour by mink in non-enriched housing.

This consistent finding of increased exploratory behaviour in mink living in non-enriched environments has interesting implications. First, it confirms that assessing non-specific exploration in a familiar environment is a worthwhile way to assess boredom-like states in barren housing, and so potentially useful for testing boredom-related hypotheses in mink and other species (including, for instance, fascinating new hypotheses about how boredom might co-vary with changes in time perception: Burn 2017). Second, this finding raises fundamental functional questions about why animals might have non-specific needs for stimulation or arousal. This includes whether maintaining moderate arousal levels is important for brain development in early life or promotes learning, as suggested by the Yerkes-Dodson law (see e.g. Burn, 2017). Third, in terms of practical on-farm welfare, it also suggests that the practice in some Scandinavian countries of selectively breeding farmed mink for exploratory responses in temperament tests (e.g. Malmkvist and Hansen, 2001) may not always be good for welfare if selection relies heavily on the response to an unfamiliar object (a stick used in one of the temperament tests). The common alternatives to exploration are aggressive or fearful responses, and some exploratory behaviour is indeed likely preferable to fear, but our data suggest that the tests as used may perhaps lead to the accidental selection for boredom-proneness. This hypothesis now needs further research: whether non-enriched mink showing the most extreme levels of interest in stimulation have the poorest welfare needs investigation, for example by looking at markers of chronic stress after long-term housing in these conditions.

A related issue is that our finding seems, at least superficially, at odds with much research on enrichment that reveals enriched animals to be bolder (see e.g. Jones and Waddington, 1992 on chicks and Meagher et al., 2014 on mink). We suggest that this may be because fear and timidity are biologically dissociable from neophilia (see e.g. Mettke-Hoffman et al., 2002; Réale et al., 2007): a distinction that might help future researchers interested specifically in boredom. Boredom is thus be easiest to detect with novel stimuli which best distinguish explorativeness from boldness, and so care should be taken to avoid the use of stimuli perceived as too similar to those experienced by subjects in enriched conditions, since habituation may be generalized. Boredom may also be easiest to assess in populations with relatively low levels of fear, such as this one, since high levels of fear are likely to override other motivations and prevent exploration. This last issue could explain why the literature currently shows conflicting evidence on the effects of enriched housing on exploratory behaviour, since some research that has suggested that enrichment can increase exploration (e.g. Acklin and Gault, 2015; Renner, 1987), the non-enriched treatments used might well have increased baseline anxiety (e.g. isolation combined with barren housing), and the tests of exploration were conducted in novel environments. By contrast, non-enriched pigs given novel objects in their home environments for longer periods of time show increased exploration relative to enriched-housed animals (e.g. Bracke and Spoolder, 2008; Stolba and Wood-Gush, 1980).

The specific stimuli used may thus be important in distinguishing between underlying states, in terms of their valence and salience. Table 3 provides information on responses to the stimuli we have employed for mink to date. Across the two studies, the moving stimulus (toothbrush) and air puff attracted the most interest (indicated by prolonged orientation and contact), and the air as well as the glove elicited fear responses, making these the most clearly aversive stimuli. The first stimulus presented, whether this had been categorized as “ambiguous” (bottle, original study) or "rewarding" (pheasant scent, replication) also elicited fear. Scents with no apparent biological relevance (vanilla and peppermint), meanwhile, attracted little attention. For future work in mustelids, we therefore recommend “chaseable" stimuli as likely rewarding, and air puffs and handling gloves as aversive. In terms of usefulness in assessing boredom, the stimuli attracting moderate interest seemed to be the most successful, as indicated by the largest housing effects on orientation and contact times (the pheasant scent, followed by the predator scents and plastic bottle, in the current study; and the female faeces and candle in the original study). Frightening (glove and air puff) and highly attractive (moving toothbrush) stimuli, by contrast, elicited high exploration, that was more universal across treatments. Thus, boredom-like elevated interest appears most pronounced for mildly rewarding and neutral/ambiguous stimuli. We therefore recommend that future research of this kind in other species begin with pilot testing to determine the typical valence of the novel stimuli on a separate group of subjects in both enriched and non-enriched conditions.

With respect to the behavioural correlates of boredom-like responses, one of the two findings from the original experiment was replicated: the positive relationship with lying still but awake. By contrast, the previous relationships with loco stereotypic behaviour were not apparent in this cohort, suggesting that stereotypic behaviour is not reliably linked to boredom in farmed mink. The confirmed link between boredom-like states and awake forms of inactivity, in which animals lie still despite being open-eyed and alert, adds to growing evidence that some forms of inactivity indicate poor animal welfare (Fureix and Meagher, 2015). It is also somewhat consistent with the human boredom literature; behavioural lethargy is considered a common symptom, although to our knowledge, to date no studies have yet investigated phenotypic subtypes of inactivity in humans that correlate with boredom. Furthermore, theoreticians have argued that states of ‘limbo’ are possible in animals, in which their physiological needs are met but they are left with time they cannot fill with motivated behaviours (McFarland, 1989). This may produce negatively-valenced states of either boredom or depression depending on the individual and/or the duration of time spent in these conditions (cf. Wemelsfelder, 1990). Our findings complement data on the awake inactivity associated with poor welfare in horses and mice, although here ‘standing doing nothing’ is hypothesised to reflect depression-like states, and in horses is linked with reduced rather than increased responsiveness to stimuli (Fureix et al., 2012; Fureix et al., 2016). Furthermore, “idle standing” is also sometimes reported as an undesirable occurrence in species such as dairy cattle (related to sickness, social competition, or uncomfortable environments: Fogsgaard et al., 2012; Huzzey et al., 2006; Rushen et al., 2007), although not yet attributed to any particular psychological state. The states underlying these other forms of awake inactivity thus now need to be investigated in a range of species.

Lying still but awake is, however, by no means a perfect indicator of boredom in mink. If used simplistically as a boredom indicator, it clearly would be prone to false negatives or Type II errors, since some individuals who were not observed performing this behaviour were still very interested in stimuli (especially in the NE mink: a crucial drawback of this measure if it is to be used on farms, for animals whose housing is more like our NE cages than our E conditions). Furthermore, in this current cohort, absolute levels of lying awake were also not significantly elevated in NE housing, despite these animals' elevated levels of boredom-like exploration: a difference from the original study indicating a group-level dissociation here between these two aspects of behaviour. However, at an individual level, lying awake in both studies was rather consistently correlated with interest in stimuli in the enriched-housed mink. If lying awake is confirmed not to correlate with interest in stimuli in mink housed in standard farm conditions, more research is needed to determine how such mink typically manifest boredom-like states.

Why some correlations with spontaneous behaviour were seen only within the enriched treatment in both experiments remains an outstanding question. While NE mink were almost universally highly exploratory in the original experiment, leaving less possibility of detecting correlations due to ceiling effects, in this replicate study variation was *not* higher in enriched than non-enriched mink for all measures of interest in stimuli. To explore this puzzle further, we recommend now replicating this study once again, but better timed to avoid any potential after-effects of the mating season.

Since identifying specific, reliable indicators of boredom-like states in the spontaneous behaviours of mink thus appears difficult, despite these intriguing relationships with awake inactivity, and since tests such as those used here are time-consuming and difficult to conduct in commercial settings, we believe that such future work could benefit from now also including qualitative behaviour assessments (QBA). The adjective “bored” is already included in some QBA protocols (e.g. Brscic et al., 2009 for veal calves), and has adequate inter-observer reliability in some species (Forkman and Keeling, 2009), although the label has not yet been validated. In factor analysis of these QBA data, it has also been linked to descriptors of activity levels (Brscic et al. 2009: negatively loaded in the same factor that included “active” and “lively” among positive loadings). We suggest that measures of elevated interest in stimuli as used here could be suitable for such a validation of these QBA labels. Reciprocally, QBA could then emerge as a useful practical way of identifying boredom in mink (since potentially less time-consuming than exploration-related tests), especially if it proved to show greater sensitivity and less proneness to false negatives than the measures of spontaneous lying awake behaviour we have used to date.

5. Conclusions

This study confirms our previous findings that long-term housing in non-enriched conditions induces increased interest in a range of stimuli in farmed mink, consistent with the presence of boredom-like states. It also broadly replicates the finding that spending more time lying still but awake is positively correlated with this state, at least among mink in enriched housing. More research is still needed to understand the conditions under which this form of inactivity could be used as a more reliable indicator of boredom, and to identify other symptoms that could be used in combination (perhaps as part of a QBA assessment). In the meantime, our results confirm that assessing the degree of responsiveness to a range of stimuli can be used to reveal boredom-like states in animals in non-enriched housing, with potential implications not just for mink, but for other species as well.

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8. Tables

Table 1. Stimuli for investigatory behaviour and treat consumption tests

Category	**Stimulus name**	**Order presented**	**Sum of fear scores**	**Mean latency to contact (s; 95% CI)[1]**
Rewarding	Pheasant scent[2]	1	2	2.9 (1.1-7.6)
Ambiguous	“Linen”-scented candle*	2	0	7.5 (2.6-21.1)
Aversive	Polar bear urine[2]	3	0	5.7 (2.3-13.9)
Ambiguous	Rope and cloth dog toy	4	0	1.5 (0.6-3.4)
Rewarding (consumption)	Cat food (Fancy Feast^{TM} chicken hearts and liver)*	5	N/A	N/A
Rewarding	Mink Lure No. 1 (Hawbaker’s^{TM})	6	0	3.6 (1.7-7.9)
Aversive	Mountain lion urine*[2]	7	0	9.4 (4.0-22.2)
Ambiguous	Vanilla scent[2]	8	0	5.9 (2.5-13.7)
Rewarding	Toothbrush moved along cage top by experimenter*	9	0	1.1 (0.5-2.8)
Aversive	Air puff*	10	2	1.7 (0.7-4.6)
Rewarding (consumption)	Hot dog sausages (diced)*	11	N/A	N/A
Ambiguous	Empty plastic bottle*	12	0	18.0 (7.3 – 44.5)
Rewarding	Duck liver treat (Pet Botanics	13	N/A	N/A

(consumption)	Healthy Omega Treats™)			
Aversive	Handling glove used on farm*	14	7	29.8 (12.3-72.4)

* Also used in original experiment; predator odour was purchased from an online source in that case, but was also urine from a wild felid (bobcat), while the candle had an “ocean” rather than “linen” scent.

[1] Back-transformed from log-transformed data.

[2] Scents were presented using round absorbent cotton pads soaked with a few drops of the liquid, inside a small wire mesh cage such that the mink could only touch the wire and not tear the cotton.

Table 2. Treatment effects in comparison with those in Meagher and Mason (2012): non-enriched relative to enriched mink

Square brackets indicate a statistical trend (0.05<*p*<0.10). NS = no significant effect (*p*>0.10). --- = not applicable because no relevant test

Spontaneous behaviour		**Interest in stimuli**				
Loco stereotypy	**Lying awake**	**Stimulus type**	**Latency**	**Orientation**	**Contact**	**Consumption**[1]
Original experiment						
Higher[2]	Higher[2]	All	Lower	Higher (but differs by stimulus)	Higher (but differs by stimulus)	---
		Aversive	Lower	NS	NS	---
		Ambiguous	Lower	Higher	Higher	---
		Rewarding	Lower	NS	NS	Higher
Current replicate experiment						
Higher	NS	All	NS	Higher (but differs by stimulus)	Higher	

Aversive	NS	Higher	Higher	---
Ambiguous	NS	Higher (but differs by stimulus)	Higher (but differs by stimulus)	---
Rewarding	NS	[Higher]	[Higher]	NS

[1] Proportion of food treats consumed.

[2] See Meagher et al. 2013 (here stereotypy data were for several cohorts pooled, including these individuals).

Table 3. Interest elicited by specific stimuli in the current replicate study and the original experiment (Meagher and Mason 2012).

		Time oriented (s)[1]		Time in contact (s)[1]		Overall interest ranking[2]	Fear elicited? (yes/no)	Effect size ranking[3]
Category	**Stimulus name**	**NE**	**E**	**NE**	**E**			
Original experiment (Meagher and Mason 2012)								
Rewarding	Brush	274.9	272.0	226.1	220.0	1	Yes	9.5
Aversive	Predator odour	210.1	178.8	196.4	162.4	2	Yes	6.5
Aversive	Air puff	178.5	163.5	125.1	106.2	3	Yes	8
Neutral	Bottle	203.6	141.9	163.0	101.3	4.5	Yes	4.5
Neutral	Maraca	213.8	151.3	153.2	91.1	4.5	No	3
Aversive	Predator silhouette	161.6	130.8	n/a	n/a	6	Yes	8
Rewarding	Faeces	183.1	102.8	172.5	88.0	7	No	2
Aversive	Glove	173.4	121.9	72.1	56.6	8	Yes	7
Neutral	Peppermint	186.7	94.2	117.1	57.8	8.5	No	3.5

Neutral	Scented candle	185.1	85.1	125.4	63.4	8.5	No	2
Replicate (current) experiment								
Aversive	Air	158.0	200.8	124.0	188.0	2.5	Yes	7.5
Neutral	Bottle	68.3	184.8	60.0	149.0	5	No	3.5
Neutral	Candle	83.8	69.8	59.0	40.7	11	No	11
Neutral	Dog toy	113.8	216.8	87.0	169.0	4	No	5
Aversive	Glove	127.6	114.8	0.0	46.7	7.5	Yes	9.5
Rewarding	Mink lure	81.5	160.5	61.0	122.7	7	No	7.5
Aversive	Mountain lion urine	64.0	164.5	49.7	155.0	7	No	3.5
Rewarding	Pheasant scent	110.8	253.0	65.0	221.0	2.5	Yes	1
Aversive	Polar bear urine	55.3	152.0	40.0	136.3	8.5	No	4.5
Rewarding	Toothbrush	294.0	295.0	277.7	281.0	1	No	9.5
Neutral	Vanilla	24.0	136.8	16.0	110.3	10	No	3.5

---

[1] Values are least squares means from general linear models (original experiment) and from MANOVAs for the replicate.

[2] Ranked within each measure of exploration (orientation and contact), then given overall ranking by averaging the two, with the highest rank (smallest number) indicating the highest durations.

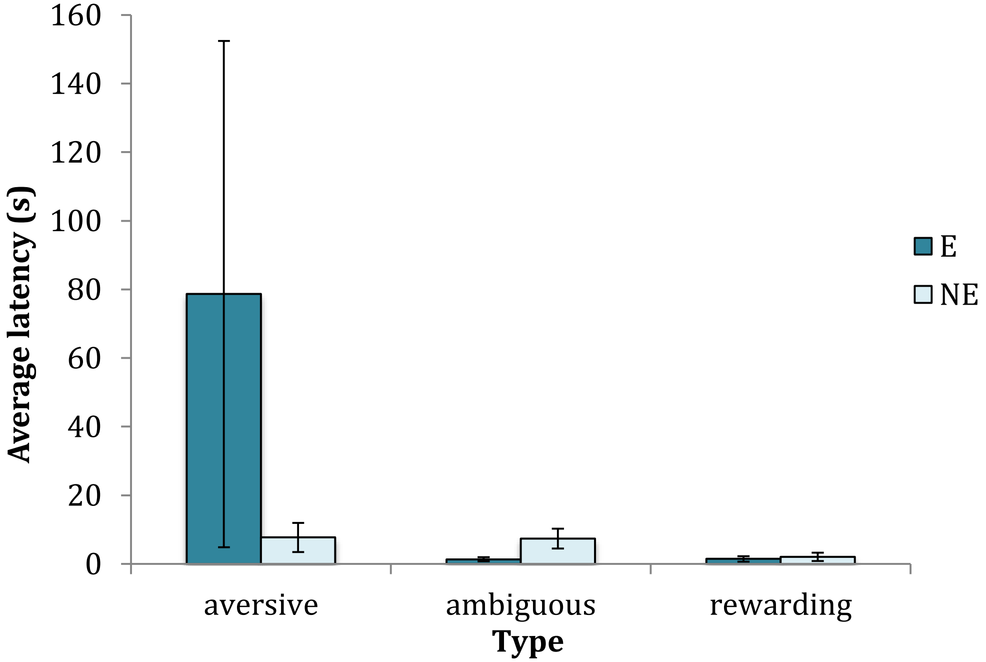
[3] Ranked within each variable (orientation and contact), then given overall ranking by averaging the two, with the highest rank (smallest number) indicating the largest difference between treatment means (non-enriched minus enriched)

Table 4. Correlations between interest in stimuli and other behaviour patterns hypothesized to reflect boredom. Original = original experiment (Meagher and Mason 2012), replicate = current experiment. NS = no significant effect (*p*>0.10). Square brackets indicate a statistical trend (0.05<*p*<0.10); these treatment-specific effects are reported where there was a significant interaction between treatment and behaviour. Neg. = negative relationship, pos. = positive. --- = not applicable because no relevant test

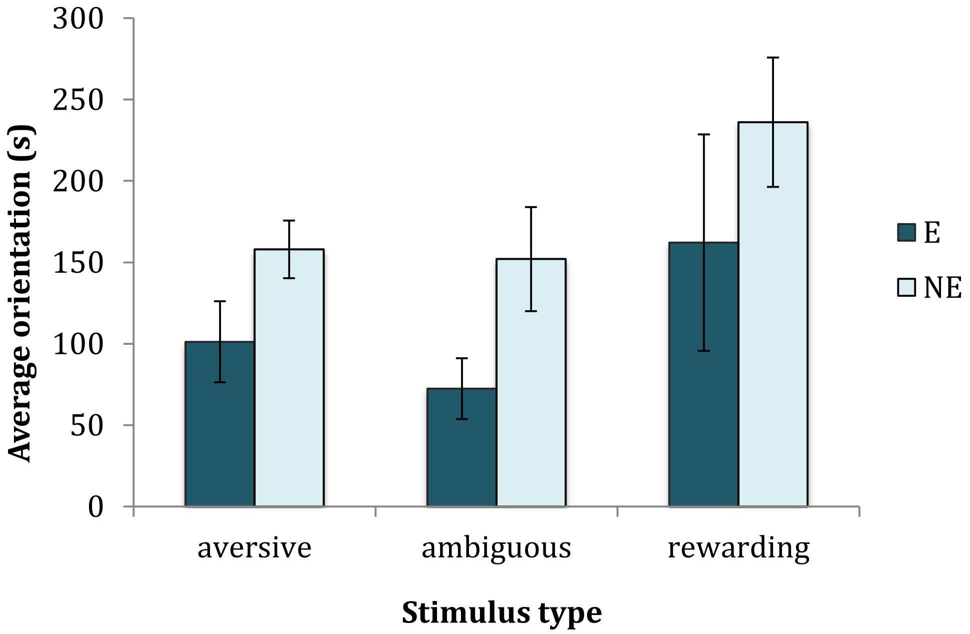
	Stimulus type							
Measure	***All***		***Aversive***		***Ambiguous***		***Rewarding***	
	Original	**Replicate**	**Original**	**Replicate**	**Original**	**Replicate**	**Original**	**Replicate**
Lying still but awake								
Latency	***Neg.***	NS	NS	NS	NS	NS	**Neg.**	**Neg.**
Duration oriented	**[E only, pos.]**	**E only, pos.**	NS	**E only, pos.**	**[E only, pos.]**	NS	NS	NS
Duration in contact	NS	**E only, pos.**	NS	**E only, pos.**	NS	**E only, pos.**	NS	NS
Treat consumption	---		---		---		**[E only, pos.]**	NS

Loco stereotypic behaviour								
Latency	NS	NS	NS	NS	NS	NS	NS	NS
Duration oriented	Interaction but each treatment NS	NS	**[E only, neg.]**	NS	NS	NS	**Neg.**	NS
Duration in contact	**[E only, neg.]**	NS	**E only, neg.**	NS	NS	NS	**Neg.**	NS
Treat consumption	**---**		**---**		---			NS

9. Figure captions



a)


300
250
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Average orientation (s)
aversive
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Stimulus type
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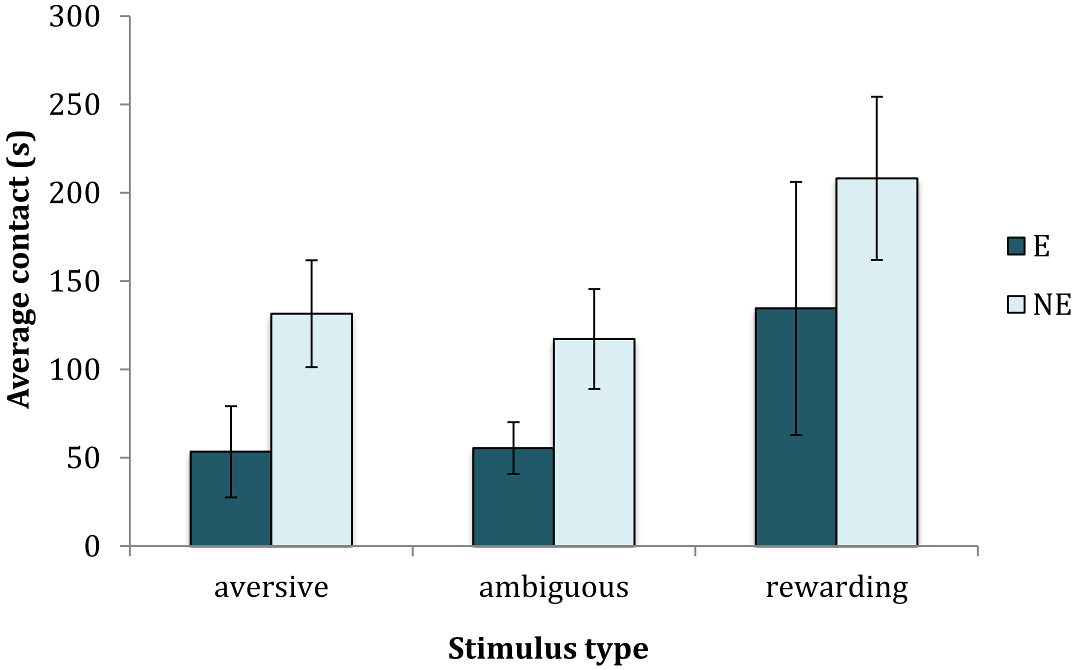
b)



c)

Figure 1. Minks' interest in stimuli by housing treatment and stimulus type. a) Latency to contact (back-transformed from log data); b) average duration oriented to stimulus over 10 minute tests; c) average duration in contact with stimulus. Values are averages of least square means for each stimulus within the categories ± SE.

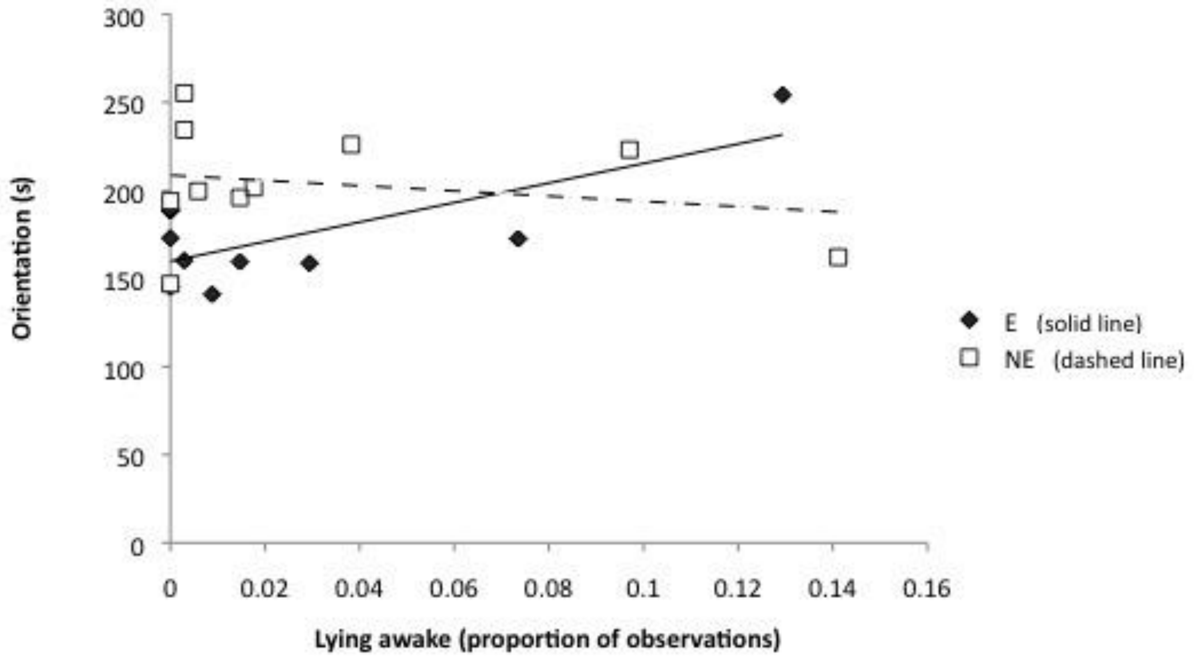


Figure 2. The duration of time mink spent oriented to all stimuli presented in the tests, regressed against the time spent lying still but awake in the home cage during scanning observations over the winter (split by housing treatment). Values on the y-axis are least squares means.

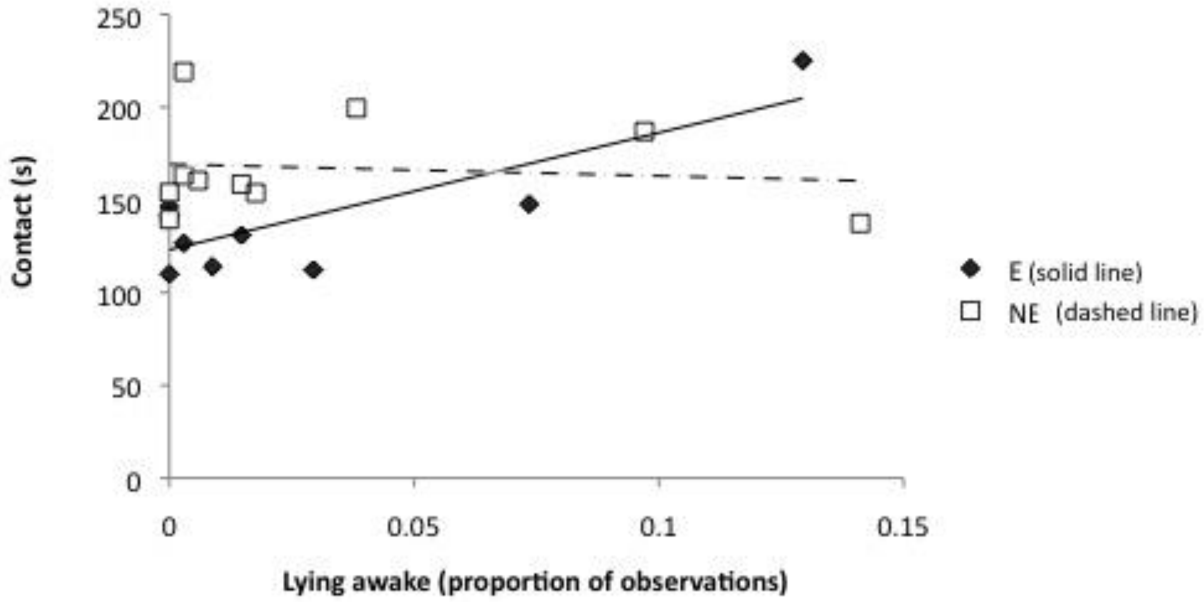


Figure 3. The duration of time mink spent in contact with all stimuli, regressed against time spent lying still but awake (split by housing treatment). Values on the y-axis are least squares means.