

**Stereotypic behaviours are heterogeneous in their triggers and treatments in the American mink (*Neovison vison*) — a model Carnivore**

Stereotypic behaviours (SBs) are common in confined animals including captive Carnivora. These display diverse forms of SB: often whole-body movements (e.g., pacing), but also head-only movements (e.g., head-twirling) and “scrabbling” (scratching at enclosure boundaries). Although often pooled together, emerging evidence indicates that SBs are heterogeneous, suggesting that subtypes differ in their causes, triggers, and consequently treatments. In mink, a model Carnivore, scrabbling seems to be elicited by neighbouring conspecifics. We tested this hypothesis *via* three studies of 32 males (individually-caged in rows, and separated by solid partitions). Study 1 investigated whether neighbour proximity affects the location of any SBs, and Study 2, whether removing neighbours reduces any SBs. Results revealed that although mink typically avoided proximity to their neighbours, scrabbling was uniquely directed towards neighbours who were close to the shared cage partition ( $Z < 3.59$ ,  $P < 0.05$ ). It was also the only SB significantly elevated by having all-male neighbours, and reduced by removing neighbours ( $Z < 2.75$ ,  $P < 0.05$ ). Study 3 then investigated whether environmental enrichment – a standard SB treatment – would reduce or abolish different SBs equally, to assess whether scrabbling is simply easier to alleviate than other SBs. Enrichment reduced all SB subtypes ( $Z = 4.38$ ,  $P < 0.05$ ), but logistic regressions revealed that the odds of complete abolition were higher for whole-body ( $OR < 10.09$ ,  $P < 0.05$ ) and head-only SBs ( $OR < 28.73$ ,  $P < 0.01$ ) than for scrabbling. Overall, these naturally solitary Carnivores thus seem to avoid conspecific proximity, but they specifically direct their stereotypic scrabbling at neighbours; and their scrabbling is reduced by neighbour-removal, while their whole-body and head-only SBs are instead better alleviated with enrichment. Understanding that Carnivore SBs are heterogeneous in their triggers and most effective treatments may help zoos, breeding centres and mink farms improve the design of their enclosures and the efficacy of their enrichments.

**Keywords:** stereotypic behaviour, American mink, animal welfare, abnormal repetitive behaviour, causation, environmental enrichment, husbandry, housing, conspecifics

Stereotypic behaviours (SBs) are repetitive behaviours common in barren environments (e.g., Mason, 1991; Shyne, 2006; Swaisgood & Shepherdson, 2005). Typically indicative of poor welfare (e.g., Gottlieb, Capitanio, & McCowan, 2013; Malmkvist, Jeppesen, & Palme, 2011; Mason & Latham, 2004), they can sometimes reflect specific forms of brain dysfunction (as reviewed by Lewis, 2004) and even predict poor reproductive success (Díez-León et al., 2013). For these reasons, as well as the poor public image they convey (e.g., in zoos, Miller, 2012), SBs are commonly used in welfare assessments (e.g., for fur-farmed mink and foxes: European Fur Breeders Association, EFBA, 2015). Likewise, in line with the World Zoo and Aquarium Animal Welfare Strategy (Mellor, Hunt, & Gusset, 2015), zookeepers, curators, and other animal care personnel typically work hard to reduce SBs by altering husbandry routines and improving enclosure complexity: a tactic that often reduces them, but rarely eliminates them (e.g., Shyne, 2006; Swaisgood & Shepherdson, 2005).

SBs, especially route-tracing, appear particularly common across the Carnivora, occurring in every major family (Clubb & Mason, 2007; Kroshko et al., 2016; Swaisgood & Shepherdson, 2005). American mink (*Neovison vison*) are ideal models for investigating Carnivore welfare and behaviour as they are populous on fur farms, allowing researchers to observe numerous animals (and potentially manipulate enclosures in ways that would be difficult in zoos). Furthermore, mink display a variety of SBs similar to those displayed by other Carnivora. Thus they show the whole-body forms typical of this taxon (e.g., pacing back and forth and whole-body bobbing: Mason, 1993; Svendsen, Palme, & Malmkvist, 2013). They also display head-only forms (e.g., head-bobbing, head-twirling, and head-weaving: Mason, 1993; Svendsen et al., 2013) that are similar to those reported in some bears (e.g., Asiatic black bears and Malayan sun bears: Tan et al., 2013; Vickery & Mason, 2004; polar bears: Ross, 2006; brown bears: Montaudouin & Pape, 2005). Finally, American mink (henceforth ‘mink’), like some other captive mustelids, can also repeatedly scratch at enclosure walls with the front paws (“scrabbling”:

Hansen & Jeppesen, 2001; Morabito & Bashaw, 2012; Polanco, Campbell, Díez-León, & Mason, 2017). We therefore used mink in a series of three experiments aimed at investigating the factors affecting these different forms of Carnivora SB.

Since the 1960s, researchers have suggested that SBs are heterogeneous (e.g., Berkson, 1967; Keiper, 1969; see also Mason, 1991, 1993; Mason & Turner, 1993). Emerging empirical evidence supports this view: SBs vary in their links with other welfare indicators (e.g., Novak, Bailoo, Melotti, & Würbel, 2016; Pomerantz, Paukner, & Terkel, 2012; Pomerantz, Terkel, Suomi, & Paukner, 2012); the degree to which different environmental contexts enhance their development (Campbell, Dallaire, & Mason, 2013; Gross, Engel, Richter, Garner, & Würbel, 2011; Jones, Mason, & Pillay, 2011; Tan et al., 2013); their epidemiological risk factors in terms of both husbandry (Bashaw, Tarou, Maki, & Maple, 2001; Greco, Meehan, Heinsius, & Mench, 2017; Waters, Nicol, & French, 2002) and species-typical behavioural biology (Kroshko et al., 2016; Pomerantz, Meiri, & Terkel, 2013); and finally, in whether they are associated with generalised behavioural inflexibility (Kirsty, Andrew, Meriel, & Catherine, 2015; Novak et al., 2016; Pomerantz, Paukner, et al., 2012). Despite this, most studies, including those of mink, still pool SBs into one single, homogeneous category (e.g., Anderson, Arun, & Jensen, 2010; Hansen, Møller, & Damgaard, 2011; Tilly, Dallaire, & Mason, 2010).

Recently, we found strong empirical evidence of SB heterogeneity in mink, with whole-body and head-only SBs negatively correlating with each other and with scrabbling, potentially suggesting three distinct subgroups with different causal bases (Polanco et al., 2017). This, in turn, suggests that diverse methods might be best for reducing or preventing these different SB subtypes. If correct, such information could help animal care personnel prevent and alleviate SBs more effectively in mink and other Carnivore species. Indeed, despite previous studies examining SB triggers across different species (see Clubb & Vickery, 2006 and Rose, Nash, & Riley, 2017 for reviews), no experiment to date has investigated the triggers of different SBs within the same species. Furthermore, we know of only two experiments to explicitly investigate the relative effectiveness of various environmental improvements on different forms of SB, neither using pre-validated SB subtypes (instead categorising SBs informally by form). Keiper

(1969, 1970), working with canaries, found that route-tracing, but not stereotypic spot-picking, was reduced by large aviary cages, swinging perches and group housing, while providing seed bells as foraging enrichments uniquely reduced spot-picking. More recently, Malmkvist, Palme, Svendsen, & Hansen (2013) found that biting ropes successfully reduced fur-chewing in mink, but not “locomotor” SBs (a category pooling whole-body and head-only SBs), even though both SBs could be reduced by supplying chunky feed. Here, we present three experiments that build on our previous work to investigate whether: 1) different SB subtypes, already well-validated as distinct subgroups (Polanco et al., 2017), differ in their environmental triggers, and 2) removing a neighbour and providing environmental enrichment are equally or differentially effective at alleviating these different SBs.

## **STUDY 1: NEIGHBOUR PROXIMITY**

One hypothesised underlying basis or trigger for some SBs is the frustration of motivations to reach resources or other animals outside of the cage. For instance, elegant experiments on laboratory mice have shown that bar-related SBs (e.g., bar-chewing and -sniffing) derive from motivations to escape the cage and/or investigate environmental cues outside it (Nevison, Hurst, & Barnard, 1999, Lewis & Hurst, 2004). Likewise, in several Carnivores, SBs can occur at boundaries separating subjects from feeding areas (Cless & Lukas, 2017) or conspecifics (Clubb & Vickery, 2006; Vickery & Mason, 2004). For instance, some farmed silver fox (*Vulpes vulpes*) and blue fox (*Alopex lagopus*) SBs are performed in parallel with those of foxes in neighbouring cages (European Commission, 2001). Likewise, pacing occurs against fences separating adult conspecifics from each other in cheetahs (*Acinonyx jubatus*: Lyons, Young, & Deag, 1997) and dingoes (*Canis lupus dingo*: Meyer-Holzapfel, 1968). In mink, males may direct SBs towards reproductively-receptive neighbouring females (along the shared cage wall), while mink mothers separated from their offspring may show SBs against the intervening barrier (Mason, 1993); and scrabbling appears particularly likely to be directed towards neighbouring animals or inaccessible cage areas (Dallaire, 2011; Hansen & Jeppesen, 2000). Such observations suggest that some Carnivore SBs represent thwarted motivations to approach conspecifics or resources, but no experiments

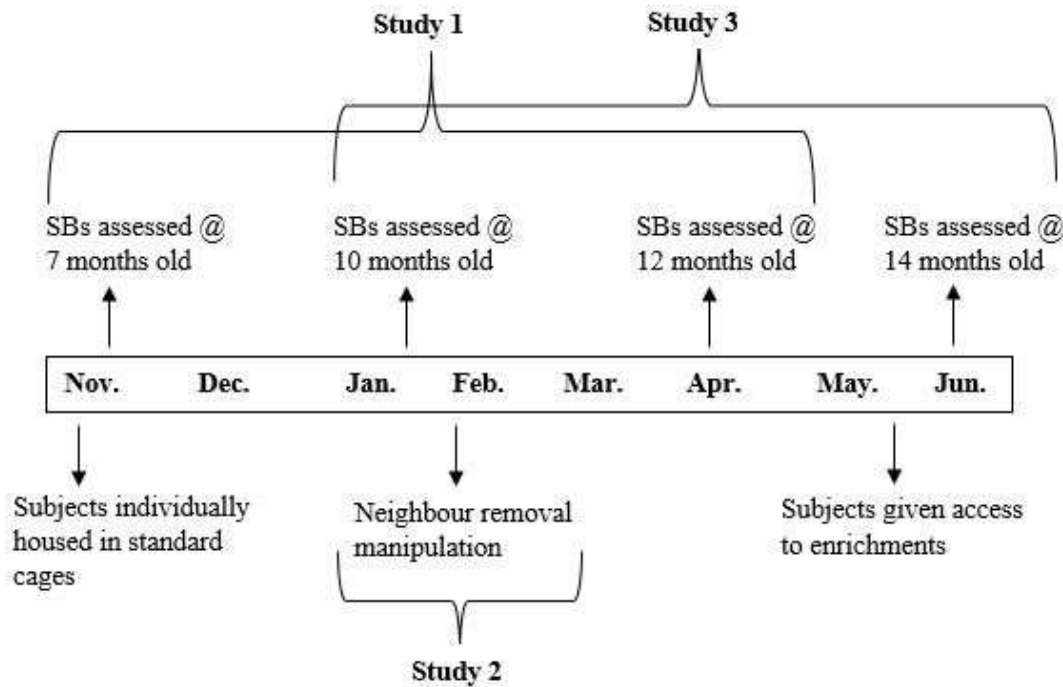
have tested this hypothesis. We therefore assessed whether any subtypes of SB represent frustrated attempts to reach neighbouring conspecifics. In this first study, we investigated the effects of neighbour number and sex on male minks' SB time-budgets. We also recorded where their SBs were performed, to assess whether the locations of any subtypes were indeed affected by neighbour proximity. If previous observations were correct, scrabbling should be particularly likely to be directed towards neighbours.

## ***Methods***

All three studies received ethical approval from the University of Guelph's Animal Care Committee (AUP 3246) and Michigan State University's Institutional Animal Care and Use Committee (AUF 12/14-226-00).

### ***Subjects and housing***

Subjects were 32 unrelated male mink housed at Michigan State University's Experimental Fur Farm (though halfway through the study when subjects were 10 months old, one mink was assigned to another project reducing the  $N$  to 31). They were individually-housed (as standard for this species) in rows of cages ( $W60\text{cm} \times L75\text{cm} \times H45\text{cm}$ ) primarily made of wire-mesh, but with side walls of opaque plastic (c. 3mm thick). Each cage had an exterior nestbox ( $W25\text{cm} \times L25\text{cm} \times H30\text{cm}$ ) and some enrichment (i.e., a shelf-like structure and a wiffle ball) to comply with Canadian Codes of Practice (National Farm Animal Care Council, 2013). Due to the facility's layout, subjects were caged either between two male neighbours ( $n = 12$ ), between one female and one male ( $n = 12$ ), or — if at the end of a row — beside one male ( $n = 4$ ) or one female ( $n = 4$ ) of the same age and colour type. Thus, 28 subjects had at least one male neighbour, while 16 had one female neighbour. Their cages' opaque plastic side walls meant they could hear and smell their neighbours, but not see them. Figure 1 gives a timeline of the three experiments.



**Figure 1. Timeline for the three studies**

### *Behavioural observations*

Following Polanco et al. (2017), behavioural data (on SBs as well as normal activity, the latter acting as a control; see Table 1) were collected live for 4h before feeding (08:00 h to 12:00 h), daily over an 8-day period when mink were 7 months old (the age they start to consistently show SBs: Jeppesen et al., 2000), and again for two 6-day periods when 10 and 12 months old. Data were always collected in the mornings, as mink SBs peak before feeding, with animals becoming inactive afterwards (e.g., Hansen et al., 2007; Mason, 1993; Svendsen, Hansen, and Jeppesen, 2007). During each scan, to score the location of each subject and his neighbours, the subject's and neighbours' home cages were virtually divided into four equal quadrants: "northwest", "northeast", "southwest", and "southeast" (see Figure 2). For the 24 subjects caged between two mink, we noted the location of the closest neighbour (e.g., if the subject was in the west part of the home cage, then only the location of the neighbour to the west of the subject was

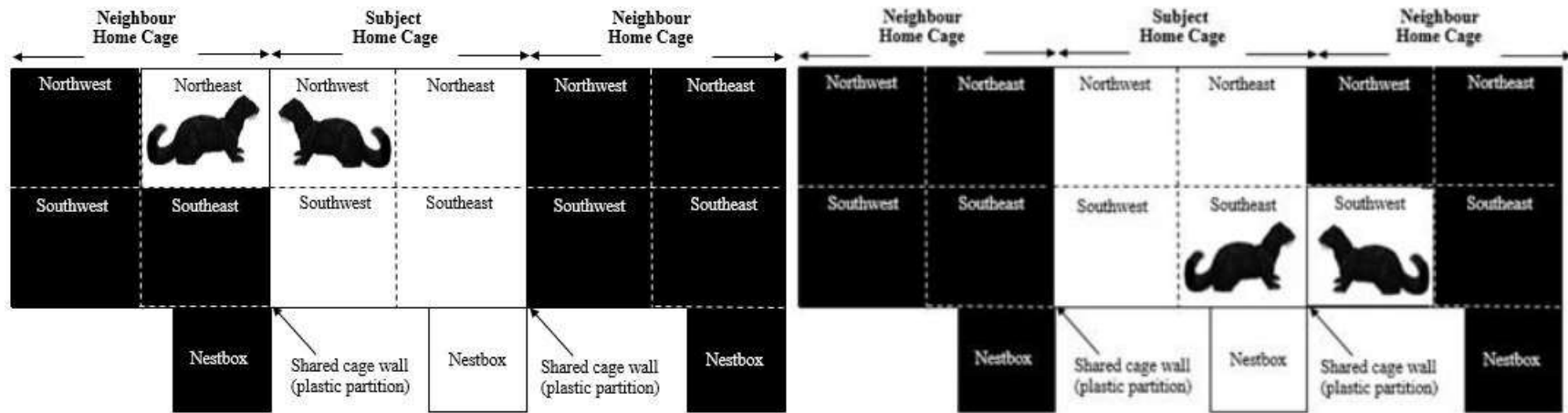
recorded). Subjects were scored as being close to neighbours if immediately adjacent to the neighbour at the time of the scan (e.g., if the subject was in the southwest quadrant of his cage and the corresponding neighbour was in the southeast quadrant of his/her cage; Figure 2). If the subject was in the centre of his home cage (a rare occurrence) or inside his nestbox, these observations were excluded because we were only interested in home cage behaviour that could unambiguously be scored as close to or far from a neighbour.

Behaviour	Description
Stereotypic behaviours	Head-only movements, including head-bobbing, head-twirling and head-weaving, repeated at least three times within a bout
	Whole-body movements including pacing back and forth along the cage wall or between the home cage and nestbox, and upper-body bobbing, repeated at least three times within a bout
	Scrabbling
	Repeatedly scratching at the cage walls with the front paws for a minimum of 5 s
Normal activity	Any non-SB activity such as eating, drinking, grooming, walking, sniffing, urinating, defecating

**Table 1. Ethogram used**

151 1)

2)



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154 **Figure 2. Scoring system used to record subject and neighbour locations, and neighbour proximity**

155 Neighbours were “close” if immediately adjacent to the subject, for example, if the subject was “northwest” and the neighbour “northeast” (1), or  
 156 if the subject was “southeast” and the neighbour “southwest” (2). In the examples above, the neighbour was not considered close if he or she was  
 157 in the areas shaded in black.



*Statistical analyses*

Data were analysed with STATA 14.2 (StataCorp, College Station, TX) and JMP 12 (SAS Institute, Cary, NC). Non-parametric tests were used as the data could not be transformed to meet parametric assumptions of homogeneity of variance. Because SB time-budgets are generally consistent from 10 to 12 months of age (Polanco et al., 2017), and since there were not enough data to analyse 10 and 12 months of age separately, we pooled data from these ages (young adulthood); but we analysed data from 7 months of age (adolescence) separately.

Before testing our hypothesis, we assessed baseline behaviour to generate descriptive statistics (e.g., the prevalence and average time-budgets of each SB subtype) and evaluate whether time-budgets differed between SB subtypes using Wilcoxon signed-rank tests. Further, we investigated whether baseline SB differed between mink with only male neighbours (versus also a female), or two neighbours (versus one), *via* Wilcoxon rank-sum tests. Additionally, to check whether any effects were specific to SBs *per se*, we assessed whether neighbour sex and the number of neighbours influenced normal activity.

To test our hypothesis about SB location, we calculated the proportion of each SB subtype occurring in a quadrant scored as “close to neighbour” (i.e., observations of that SB subtype performed close to a neighbour/total observations of that SB subtype). Additionally, we assessed whether neighbour proximity affected the proportion of normal activity performed close by in the home cage. Because each quadrant was  $\frac{1}{4}$  of the home cage, the probability of a subject and neighbour being in adjacent quadrants if moving at random was 0.125 ( $2*[0.25*0.25]$ ). Thus the null hypothesis was that subjects would allocate 12.5% of each behaviour to a quadrant close to a neighbour, with significantly greater proportions indicating a preferential use of such quadrants. The proportions of each behaviour located “close to neighbour” were therefore compared to 0.125, using one-sample Wilcoxon signed-rank tests. Separate Wilcoxon tests were also run based on the sex of the neighbour, here and in the subsequent study, as initial results suggested sex effects (see below).

184           Additionally, we conducted *post hoc* exploratory analyses on our SB location data. These  
185 analyses focussed on the subset of individuals who performed more than one SB subtype ( $n = 13$ ), to  
186 assess whether subjects with differential responses to the captive environment perform different SBs or  
187 instead whether, even *within* an individual, different SBs are subject to different motivational influences.  
188  $P$  values were considered significant if  $< 0.05$  and trends if  $\geq 0.05$  and  $\leq 0.10$ .

## 190 **Results**

### 191 *Descriptive Statistics*

192 Table 2 presents prevalence and time-budget data. At both 7 and 10-12 months of age, scrabbling was the  
193 most common SB subtype (being the most time-consuming SB for 18-26 mink), followed by head-only  
194 SBs (the most time-consuming subtype for 5-7 mink) and whole-body SBs (the most time-consuming  
195 subtype for 1-3 mink). Further tests revealed that these time-budget differences were statistically  
196 significant. At 7 months, stereotyping mink ( $n = 32$ ) spent significantly more time scrabbling than  
197 performing head-only SBs ( $Z = 3.82$ ,  $P = 0.0001$ ) or whole-body SBs ( $Z = 4.55$ ,  $P < 0.0001$ ). The time-  
198 budgets of head-only and whole-body SBs, however, did not significantly differ ( $Z = 0.45$ ,  $P = 0.65$ ).  
199 Similarly, at 10-12 months, stereotyping mink ( $n = 28$ ) spent significantly more time scrabbling than  
200 performing head-only SBs ( $Z = 2.28$ ,  $P = 0.02$ ) or whole-body SBs ( $Z = 3.20$ ,  $P = 0.001$ ), while the latter  
201 two subtypes did not differ ( $Z = 0.33$ ,  $P = 0.75$ ).

204	<i>Descriptive Statistic</i>	<i>SB subtype</i>		
205	<b>Prevalence of SB<sup>1</sup></b>	Scrabble	Head-only	Whole-body
206	7 months old	94%	19%	19%
207	10-12 months old	84%	32%	32%
208	<b>Median and IQR (% of observations)</b>			
209	7 months old	5% (2-7%)	0 (0%)	0 (0%)
210	<i>Only mink with that subtype</i>	5% (2-7%) <sup>2</sup>	5% (1-8%) <sup>3</sup>	2% (0.7-2%) <sup>3</sup>
211	10-12 months old	4% (3-9%)	0 (0-2%)	0 (0-0.3%)
212	<i>Only mink with that subtype</i>	5% (3-9%) <sup>4</sup>	2% (2-5%) <sup>5</sup>	2% (0.3-4%) <sup>5</sup>

213 <sup>1</sup> based on entire sample size (7 months old:  $n = 32$ ; 10-12 months old:  $n = 31$ )

214 <sup>2</sup>  $n = 30$

215 <sup>3</sup>  $n = 6$

216 <sup>4</sup>  $n = 26$

217 <sup>5</sup>  $n = 10$

218 **Table 2. Descriptive statistics for SB subtypes in stereotyping mink at 7 months old ( $n = 32$ ) and 10-**  
219 **12 months old ( $n = 28$ )**

220

221 *Neighbour effects on the time-budgets of SBs and normal activity*

222 Mink with all-male neighbours showed more scrabbling ( $Z = -2.35$ ,  $P = 0.02$ ) than mink with only female  
223 neighbours or a mix of male and female, but head-only ( $Z = 0$ ,  $P = 1$ ) and whole-body SBs ( $Z = 1.18$ ,  $P =$   
224  $0.24$ ) appeared unaffected by neighbour sex. Likewise, normal activity was not significantly affected by  
225 neighbour sex ( $Z = 1.13$ ,  $P = 0.26$ ). In contrast, neighbour number affected neither scrabbling ( $Z = 1.08$ ,  $P =$   
226  $0.28$ ), nor head-only SBs ( $Z = 0$ ,  $P = 1$ ), nor whole-body SBs ( $Z = 1.60$ ,  $P = 0.11$ ); while mink with two  
227 neighbours showed less normal activity than mink with only one ( $Z = 2.10$ ,  $P = 0.04$ ).

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*Effects of neighbour proximity on the locations of SBs and normal activity*

The proportion of normal activity performed close to female neighbours was not significantly different from chance when mink were adolescent, but tended to be lower than chance in adulthood. Likewise, this class of behaviour was significantly unlikely to occur near male neighbours when subjects were adults: only 4% of all normal activity occurred in a quadrant near a male neighbour at 10-12 months of age (Table 3).

The proportion of scrabbling located close to a neighbour was, in contrast, significantly higher than chance, with 50-89% being performed in cage quadrants close to a neighbouring conspecific (see Table 3). The location of head-only SBs was not significantly affected by neighbour proximity; however, whole-body SBs were significantly likely to be located away from neighbours in older mink (the  $n$  being too small for analysis when mink were younger).

These effects were preserved in *post hoc* exploratory analyses on the subset of individuals who performed more than one SB subtype ( $n = 13$ ), such that scrabbling was still directed towards neighbours ( $Z < 2.28$ ,  $P < 0.05$ ) while other SB forms were either still not significantly influenced by neighbours (head-only SBs:  $Z < -0.69$ ,  $P > 0.10$ ) or directed away from neighbours (whole-body SBs:  $Z < -2.25$ ,  $P < 0.05$ ).

248 **A) Effects of male neighbour proximity**

	7 months old				10-12 months old			
	<i>n</i>	Median proportion performed in quadrant “close to neighbour” (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value	<i>n</i>	Median proportion performed in quadrant “close to neighbour” (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value
Normal Activity	28	0.06 (0.01-0.17)	-1.62	0.11	28	0.04 (0-0.14)	-2.11	<b>0.035</b>
Scrabble	20	0.66 (0.29-1)	3.58	<b>0.0003</b>	21	0.75 (0.17-1)	3.35	<b>0.0008</b>
Head-only SBs	4	0.31 (0-0.81)	0.74	0.46	7	0 (0-0.12)	-1.21	0.23
Whole-body SBs	3 <sup>1</sup>	-----	-----	-----	6	0 (0-0)	-2.45	<b>0.01</b>

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250 **B) Effects of female neighbour proximity**

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	7 months old				10-12 months old			
	<i>n</i>	Median proportion performed in quadrant “close to neighbour” (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value	<i>n</i>	Median proportion performed in quadrant “close to neighbour” (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value
Normal Activity	16	0.12 (0.04-0.23)	0.41	0.68	16	0.08 (0.02-0.14)	-1.66	<b>0.098</b>
Scrabble	9	0.89 (0.43-0.93)	2.31	<b>0.02</b>	9	0.50 (0.09-0.50)	1.97	<b>0.048</b>
Head-only SBs	3 <sup>1</sup>	-----	-----	-----	4	0 (0-0.15)	-0.38	0.71
Whole-body SBs	2 <sup>1</sup>	-----	-----	-----	4	0 (0-0)	-2	<b>0.046</b>

252 *Note: Numbers differ between analyses as mink not performing each behaviour type were excluded.*

253 *Significant or trending p-values are shown in bold.*

254 <sup>1</sup> *n too small for analysis*

**Table 3. The proportions of normal activity and each SB subtype performed in cage quadrants close to male or female neighbours, compared to chance levels (0.125) using one-sample Wilcoxon signed-rank tests**

## **STUDY 2: NEIGHBOUR REMOVAL EXPERIMENT**

In addition to observational studies reporting *where* SBs occur, some research has investigated whether SB time-budgets are affected by neighbour proximity. In naturally solitary species like the okapi (*Okapia johnstoni*), head-rolling is higher when there is visual access to conspecifics (Troxell-Smith and Miller, 2016). Likewise in the Carnivora, pacing is often higher in naturally solitary species that can view conspecifics (e.g., cheetahs [*Acinonyx jubatus*]: Quirke et al., 2012; tigers [*Panthera tigris*]: Rouck et al., 2005), but is lowered by visual barriers (e.g., tigers: Miller, Bettinger, & Mellen, 2008). However, SBs can also increase when conspecifics are out of sight (e.g., in polar bears [*Ursus maritimus*]: Kelly et al., 2015) or when visually isolated from each other (*via* opaque barriers; e.g., tigers: Bashaw et al., 2007). These contradictory findings could reflect many factors, including the sex of the subjects and their neighbours, that visual isolation does not ensure complete sensory isolation from conspecifics, and individual differences in the SB subtypes performed. In mink, if neighbour proximity truly triggers scrabbling, as indicated by Study 1, then experimentally removing neighbours should reduce this SB subtype.

## **Methods**

Subjects and housing were as in Study 1, but all animals were 10 months old when these data were collected. To investigate effects of neighbour presence on subject behaviour, we removed one neighbour per subject by giving him or her voluntary access to an enriched compartment (as described in the next study), into which this animal was then locked for approximately 4 hours (from 08:00 h to 12:00 h) on one day. In total, we removed 15 female and 16 male neighbours. For the 24 mink with two neighbours, we removed only one because only half of the facility's cages had access to an enriched compartment.

## *Behavioural Observations*

We collected baseline behavioural data (*cf.* Table 1) during one 6-day period when mink were 10 months old (as in Study 1) from 08:00 h to 12:00 h. We conducted the neighbour removal manipulation two days later using the same data collection methods as Study 1 (i.e., observations occurred from 08:00 h to 12:00 h over the course of one morning). Behaviours in the nestbox were excluded from analyses to be consistent with Study 1.

## *Statistical Analyses*

Again, data were analysed with STATA 14.2 (StataCorp, College Station, TX), using non-parametric tests since parametric assumptions were unmet. To test our prediction that scrabbling would be the only behaviour affected by the manipulation, we used Wilcoxon signed-rank tests to compare the time-budgets of each SB subtype (i.e., observations of SB subtype/total number of observations) pre- and post-neighbour removal, split by the sex of the removed neighbour. Again, we conducted *post hoc* analyses focusing on the subset of 13 individuals who performed more than one SB subtype. As a control, we also assessed whether the time spent performing normal activity (i.e., observations of all normal behaviours/total number of observations) was affected by the manipulation.

To evaluate the efficacy of removing a neighbour as a treatment for SB, we ran a mixed logistic regression to see whether SB subtype predicted SB abolishment post-treatment (yes/no) with “yes” indicating that performance of the SB ceased post-treatment (at least during the pre-feed period assessed) and “no” indicating continued performance (even if at reduced levels). We included mink ID as a random effect and neighbour sex as a blocking factor. Homoscedasticity and normality of the best linear unbiased predictions (BLUPs) were assessed graphically.

## ***Results***

### *Effects of removing a neighbour on the time-budgets of SBs and normal activity*

Removing both male and female neighbours significantly reduced the time spent scrabbling. Removing female neighbours tended to reduce head-only SBs. Whole-body SBs appeared unaffected by the manipulation (see Table 4). However, the same patterns could not be detected in the 13 mink with more than one SB subtype ( $Z < 1.22$ ;  $P > 0.10$ ), although this may reflect low power. The time spent performing normal behaviours also appeared unaffected by removing a neighbour (Table 4).

	Male Neighbours				Female Neighbours			
	<i>n</i>	Median (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value	<i>n</i>	Median (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value
Normal Activity	16	Baseline 0.23 (0.18-0.30) Removed 0.20 (0.10-0.28)	0.62	0.53	15	Baseline 0.24 (0.20-0.35) Removed 0.20 (0.10-0.33)	0.63	0.53
Scrabble	16	Baseline 0.09 (0.04-0.15) Removed 0.03 (0-0.08)	2.74	<b>0.006</b>	10	Baseline 0.04 (0.03-0.07) Removed 0.03 (0-0.03)	2.09	<b>0.04</b>
Head-only SBs	6	Baseline 0.05 (0.04-0.05) Removed 0.02 (0-0.10)	0.94	0.35	4	Baseline 0.06 (0.02-0.19) Removed 0 (0-0.10)	1.83	<b>0.07</b>
Whole-body SBs	4	Baseline 0.03 (0.01-0.04) Removed 0.03 (0-0.20)	-0.73	0.47	4	Baseline 0.05 (0.006-0.10) Removed 0.03 (0-0.13)	0.14	0.89

*Note: Numbers differ between analyses as mink not performing each behaviour type during baseline were excluded. Significant or trending p-values are shown in bold.*

**Table 4. Wilcoxon signed-rank tests comparing normal activity and each SB subtype as proportions of observations when male and female neighbours were in their home cages versus “removed”**

*Effect of SB subtype on SB abolition by neighbour removal*

Within the subjects performing each particular SB subtype, 46% of scrabblers stopped performing this subtype after neighbour removal; 60% of mink with head-only SBs stopped performing this subtype; and 44% of subjects with whole-body SBs stopped performing this subtype. However, the mixed logistic regression revealed no significant effect of SB subtype on the odds of abolition ( $\chi^2 [2] = 0.28$ ,  $P = 0.87$ ).



Furthermore, the sex of the removed neighbour had no significant effect on the odds of SB abolition ( $\chi^2[1] = 0.51, P = 0.47$ ). Table 5 gives details.

Variable	<i>B</i>	SE	Odds Ratio	95% CI for Odds Ratio	<i>P</i>
SB Subtype: <i>Scrabble (referent)</i>					
Head-only SBs	-0.45	1.11	0.63	0.07-5.62	0.68
Whole-body SBs	-0.55	1.18	0.58	0.06-5.77	0.64
Neighbour Sex: <i>Female (referent)</i>					
Male	-0.81	1.13	0.45	0.05-4.07	0.47

Note: Overall model significance:  $\chi^2(3) = 0.67, P = 0.88$

**Table 5. Mixed logistic regression model assessing predictors of SB abolition during the neighbour-removal treatment ( $n = 28$ )**

### STUDY 3: EFFECTS OF ENVIRONMENTAL ENRICHMENT

Previous research has shown that head-only and whole-body SBs (pooled into one category) and scrabbling are both reduced if mink are raised in large enriched enclosures. However, only the former remain low if enriched-raised mink are transferred to small barren cages while scrabbling instead increases (Díez-León et al., 2016). Moreover, high levels of head-only and whole-body SBs (pooled) predict poor mating success in males, while scrabbling does not (Díez-León et al., 2013). Together, this led us to hypothesise that head-only and whole-body SBs reflect long-term alterations in behavioural organisation, perhaps mediated by changes in brain function (*cf.* Lewis, 2004), but that scrabbling reflects more readily reversible effects of motivational frustration (Díez-León et al., 2016). If correct, scrabbling would be easier to treat than head-only and whole-body SBs (i.e., declining to low levels at faster rates whenever conditions improve), as it would not be a product of long-term neurological changes. This view provides an alternative explanation for Study 2's results: that they do not indicate a specific effect of neighbours on scrabbling, but instead merely that this SB subtype is more labile than others.

To investigate this possibility, we gave our subjects a standard SB treatment, environmental enrichment (EE). EE comprises sensory, cognitive, physical, and/or manipulable stimuli meant to improve captive animals' welfare (e.g., Swaisgood & Shepherdson, 2005). We used enriched compartments previously shown (albeit in a modified form, see Methods below) to reduce the development of all SB subtypes in mink (e.g., Campbell et al., 2013; Dallaire et al., 2012; Díez-León et al., 2013, 2016; Hansen et al., 2007; Meagher & Mason, 2012; Meagher et al., 2013) and to be highly preferred (mink being willing to pay costs to access such enrichments: Dallaire et al., 2012; Mason, Cooper, & Clarebrough, 2001). The primary purpose of this last experiment was to assess whether different SB subtypes vary in the degree to which EE reduces or even abolishes them. If EE had a greater effect on scrabbling than on head-only and whole-body forms, then this would suggest that Study 2's results did not reflect a specific effect of conspecific proximity, but instead were just a by-product of scrabbling being easier to alleviate. Opportunistically, this study also allowed us to test a second hypothesis. One previous mink study found that a reduction in head-only and whole-body SBs (pooled) in enriched housing was predicted not by active enrichment use, but instead by the previously highly-stereotypic individuals spending more time resting in the towers and tunnels of their new enclosures (Dallaire et al., 2012). Inspired by this, we therefore collected subsidiary data on our minks' enrichment use and resting behaviour after transfer to enriched cages to see if either predicted how successfully EE reduced any of the three SB subtypes.

## **Methods**

The same subjects were given access to enriched compartments (as also used to remove neighbours in Study 2) when 14 months old. Their layouts were as described in prior research (e.g., Dallaire et al., 2012 and Díez-León et al., 2013), although the contents differed. In this study, a tunnel connected to the standard cage could be opened, giving subjects access to climbing opportunities, an elevated tunnel with an aerial view of the facility, and a large enriched compartment containing manipulable toys (e.g., hanging ropes/towels, plastic toys, and brushes) and shelf-like structures (e.g., wire-mesh 'tunnels' and a plastic toy bucket that the mink typically lay in). However, unlike prior research using the same facility,

we did not provide channels of running water for mink to swim in. Half of the mink ( $n = 15$ ) were given access to these resources earlier in another study, while the remainder ( $n = 16$ ) were given access 13 days later. Regardless, each enriched compartment was consistent across subjects and throughout the study.

### *Behavioural observations*

While mink were still in their standard cages, we collected behavioural data (*cf.* Table 1) throughout two 6-day periods at 10 and 12 months (from 08:00 h to 12:00 h), subsequently pooled for analyses (as in Study 1). After subjects were given access to enriched housing, we collected data again during an 8-day period from 08:00 h to 12:00 h, using the same methods as before but additionally recording presence in enriched housing (i.e., any time spent in the enriched areas, including the towers and tunnel), enrichment manipulation (i.e., any interaction with enrichment items), and inactivity in the towers/tunnels. To be consistent with the prior two studies, behaviours in the nestbox were excluded.

### *Statistical analyses*

Data were again analysed with STATA 14.2 (StataCorp, College Station, TX) and unless otherwise stated, non-parametric tests were used. One subject never entered his enriched enclosure and was therefore excluded from analyses. Our first objective was to investigate whether EE differentially affected the different SB subtypes. Here we used Wilcoxon signed-rank tests to compare the time-budgets of each SB subtype (i.e., observations of SB subtype/total number of observations) pre- and post-EE (also assessing whether the time spent performing normal activity was affected by EE). Like Study 2, we additionally ran a mixed logistic regression to see whether a SB's subtype predicted whether it would be abolished by EE (yes/no) with "yes" indicating that performance of the SB ceased post-treatment (at least during the pre-feed period assessed) and "no" indicating that it continued (even if at reduced levels). We included mink ID as a random effect and EE access time (early/late) as a blocking factor. We ran an additional logistic model with time spent stereotyping in standard housing as a covariate to see whether any effect of SB subtype in the first model remained significant, since baseline SB time-budgets differed

by subtype (see Study 1) and this could have explained our first model outputs. Again, we assessed homoscedasticity and normality of the BLUPs graphically and conducted *post hoc* analyses on the subset of 13 individuals who performed more than one SB subtype.

Our second objective was to investigate whether the subtype of baseline SB predicted how mink utilised their new enclosure, to potentially replicate and extend Dallaire and colleagues' (2012) findings. To do this, we ran Spearman correlations between the time-budgets of each SB subtype pre-EE and the following behaviours post-EE: inactivity in the towers/tunnels, presence in enriched housing, and enrichment manipulation. Additionally, classifying subjects by their most common (i.e., time-consuming) SB during baseline, we ran Kruskal-Wallis tests to investigate whether such mink differed in their utilisation of the new resources and enrichment behaviours.

## **Results**

### *Enrichment effects on the time-budgets of SBs and normal activity*

EE significantly reduced all three SB subtypes (Table 6). Normal activity was not reduced, but instead tended to increase.

	<i>n</i>	Median proportion (+ interquartile range)	<i>z</i> test statistic	<i>P</i> value
Normal Activity	30	NE 0.21 (0.15-0.30) EE 0.26 (0.20-0.31)	-1.70	<b>0.089</b>
Scrabble	26	NE 0.05 (0.03-0.09) EE 0.01 (0.006-0.02)	4.37	<b>&lt;.0001</b>
Head-only SBs	10	NE 0.02 (0.02-0.05) EE 0 (0-0)	2.80	<b>0.005</b>
Whole- body SBs	10	NE 0.02 (0.003-0.04) EE 0 (0-0.004)	2.81	<b>0.005</b>

*Note: Numbers differ between analyses as mink not performing each behaviour type during baseline were excluded. Significant or trending p-values are shown in bold.*

**Table 6. Wilcoxon signed-rank tests comparing time-budgets of normal activity and each SB subtype in non-enriched (NE) conditions *versus* when given environmental enrichment (EE)**

*Effect of SB subtype on SB abolition by enrichment*

31% of scrabblers ceased performing this subtype after enrichment-provision, as did 80% of mink with head-only SBs and 70% of mink with whole-body SBs; and the mixed logistic regression revealed a significant effect of SB subtype on the odds of abolition by EE ( $\chi^2 [2] = 16.34, P = 0.003$ ), this being significantly higher for head-only and whole-body SBs than for scrabbling. This result held even after controlling for time spent stereotyping in non-enriched housing (which also had a significant, independent effect:  $\chi^2 [1] = 9.93, P = 0.0016$ ). The 13-day difference in enriched access had no significant effect in either model ( $\chi^2 [1] < 1.52, P > 0.10$ ). Table 7 gives details. As in Study 2, the effects of SB subtype became non-significant when focussing only on the 13 mink with more than one SB subtype ( $\chi^2 [2] < 3.13, P > 0.10$ ).

A)

Variable	<i>B</i>	SE	Odds Ratio	95% CI for Odds Ratio	<i>P</i>
SB Subtype: <i>Scrabble (referent)</i>					
Head-only SBs	2.69	0.83	14.70	2.91-74.30	<b>0.001</b>
Whole-body SBs	2.24	0.72	9.41	2.30-38.55	<b>0.002</b>
EE Access: <i>Early (referent)</i>					
Later	0.67	0.59	1.96	0.62-6.24	0.25

Note: Overall model significance:  $\chi^2(3) = 16.71$ ,  $P = 0.0008$

B)

Variable	<i>B</i>	SE	Odds Ratio	95% CI for Odds Ratio	<i>P</i>
SB Subtype: <i>Scrabble (referent)</i>					
Head-only SBs	3.36	1.23	28.72	2.59-318.05	<b>0.006</b>
Whole-body SBs	2.31	0.95	10.08	1.57-64.68	<b>0.015</b>
EE Access: <i>Early (referent)</i>					
Later	0.91	0.74	2.49	0.58-10.71	0.22
SB time-budget in NE housing	-0.52	0.16	0.60	0.43-0.82	<b>0.002</b>

Note: Overall model significance:  $\chi^2(4) = 16.98$ ,  $P = 0.0019$

Model A includes SB subtype and EE group as predictor variables, while Model B includes time spent stereotyping in standard housing as an additional predictor (to control for scrabbling being more time-consuming: see Study 1). Significant p-values are shown in bold.

**Table 7. Mixed logistic regression models assessing predictors of SB abolition ( $n = 28$ )**

# *Pre-enrichment levels of SB and post-enrichment behaviours*

We found no significant relationships between pre-EE levels of SB and the time spent in any of the enriched areas or actively using enrichments. However, there was an unexpected significant negative correlation between pre-EE levels of head-only SBs and the time spent inactive in the towers and tunnels (see Table 8). Likewise, there were no significant differences between mink favouring the three SB subtypes in the time they spent in enriched housing ( $\chi^2 [2] = 1.41, P = 0.49$ ), using enrichments ( $\chi^2 [2] = 1.69, P = 0.43$ ), or showing inactivity in the towers and tunnels ( $\chi^2 [2] = 0.003, P = 0.99$ ).

## *EE Behaviour*

<i>SB Subtype</i>	<i>Presence in enriched housing</i>	<i>EE manipulation</i>	<i>Inactivity in towers/tunnels</i>
1. Scrabble ( <i>n</i> = 26)	+0.19	-0.26	-0.09
2. Head-only ( <i>n</i> = 10)	-0.53	+0.52	<b>-0.90*</b>
3. Whole-body ( <i>n</i> = 10)	-0.05	-0.27	+0.21

*Note: Numbers differ between analyses as mink not performing each SB subtype during baseline were excluded.*

*\*P < 0.05*

**Table 8. Spearman correlations for time-budgets of baseline SB subtypes and behaviours when given EE**

## **GENERAL DISCUSSION**

Our results demonstrate that Carnivora SBs are heterogeneous in both their triggers and their most effective treatments. They also show that caged male mink are sensitive to neighbour effects, and provide new insights into what makes some SBs more ‘treatable’ than others. Here, we discuss these findings’ implications for the welfare of mink and other Carnivora and outline key future research directions.

Given its unequivocal results, we first consider our findings on scrabbling: the SB in which mink scratch or dig at cage walls with their forepaws.

Scrabbling was the SB subtype displayed to the greatest extent by mink with all-male neighbours, and the only SB subtype to be significantly reduced by removing any type of neighbour. It was also uniquely directed towards active, nearby conspecifics in terms of its location within the cage. In this regard, mink seem to differ from other Carnivore species, which generally show pacing when displaying SB towards inaccessible conspecifics (e.g., Lyons, Young, & Deag, 1997; Meyer-Holzapfel, 1968). However, this may reflect scrabbling being quite uncommon in other Carnivora. Speculatively, scrabbling might perhaps be restricted to those species which naturally dig, such as other mustelids (e.g., otters: Morabito & Bashaw, 2012) and foxes (Korhonen & Huuki, 2011). In our subjects, scrabbling was also the SB subtype least likely to be abolished by EE: a result consistent with long-term differentially housed mink, in which EE was less effective at reducing scrabbling than whole-body and head SBs pooled (Campbell et al., 2013). This demonstrates that scrabbling is not merely more sensitive to housing changes than other SB subtypes (*cf.* Díez-León et al., 2016), and that its marked reduction in Study 2 did specifically reflect a role of strong motivations to interact with neighbouring animals. In terms of precisely what these strong motivations to interact represent, more research is needed (see below). However, we suspect that these motivations are not playful, because play in 10-12-month-old mink is rare (Ahloy Dallaire & Mason, 2016; Hansen et al., 1997); instead, we hypothesise that they are agonistic, as aggression in mink often develops around 5-6 months of age (Hansen, 1996) and sub-adult and adult males naturally compete over territory in the wild (Dunstone, 1993).

Turning to whole-body SBs, like normal activity this type of behaviour was performed in locations away from neighbours. However, avoiding conspecifics did not seem to be their primary underlying motivation: their time-budgets were not significantly affected by neighbour sex or number and experimentally removing neighbours did not reduce them. Instead, EE readily abolished these SBs: 7 of the 10 affected



subjects ceased to show them in our post-enrichment observations. Such whole-body SBs are typical for captive Carnivora, although they were the least prevalent and time-consuming SB subtype in our mink. Moreover across Carnivora, the time-budgets of route-tracing – the most common whole-body SB – are systematically highest in species with large annual home ranges (Clubb & Mason, 2003, 2007; Kroshko et al., 2016). This helps explain their low levels in mink (a species with naturally small home ranges), and also suggests that they may derive from the location-shifting normally shown when resources are locally suboptimal (a behaviour most marked in wide-ranging species: Clubb & Mason, 2007). That mink in our study could move freely between the standard and enriched cage could perhaps mimic this natural degree of choice, with this then contributing to SB reduction and, in some mink, abolition.

Lastly, we discuss our findings for head-only SBs. The time-budgets of this subtype were not affected by neighbour sex, number, and presence, nor were their locations affected by neighbour proximity. Removing a female neighbour tended to reduce them, but we suspect this to be a Type I error because removing male neighbours had no similar effect, and there was no other evidence of neighbour effects. Head-only SBs were instead similar to whole-body SBs in being more likely than scrabbling to be abolished by EE in Study 3. However, it is unclear from where head-only movements derive. In rhesus macaques, head-twirling and head-tossing (but not whole-body SBs) positively covary with behavioural inflexibility in extinction tasks, potentially suggesting brain dysfunction (Pomerantz, Paukner, et al., 2012). However, our attempts to replicate such findings in mink (using a different test) were not successful (Polanco, 2016). Below we suggest some future research that may help clarify the aetiology of these movements.

Together, these findings provide the first demonstration for *a priori* validated SB subtypes that distinct forms are both differentially triggered by stimuli like conspecifics, and also variable in the treatments most likely to reduce or abolish them. Furthermore, in our *post hoc* exploratory analyses of the subset of 13 subjects displaying more than one SB subtype, the neighbour location effects of Study 1 were

524 preserved. This therefore cautiously provides the first ever evidence that different forms of SB may differ  
525 in their motivational influences even when performed by the same subject.

526  
527 Some other findings emerged incidentally from our data. We showed that less time-consuming SBs were  
528 easier to eliminate with EE. This new result adds to previous evidence that SBs are more effectively  
529 reduced by EE if subjects are relatively young (e.g., Hadley, Hadley, Ephraim, Yang, & Lewis, 2006;  
530 Tilly et al., 2010), and also if more motivated to access EE (e.g., Tilly et al., 2010). However, we did not  
531 find that SBs were more likely to be alleviated in animals who interacted most with enrichments (*cf.*  
532 Lumeij & Hommers, 2008) or rested most in their new enclosures (*cf.* Dallaire et al., 2012). This could  
533 reflect low power or, instead, that mere use is not a sensitive measure of value (measures of strength or  
534 preference being better: Tilly et al., 2010, Dallaire et al., 2012). More research is thus needed to  
535 determine how the perceived value of enrichments affects how readily captive animals' SBs are abolished  
536 by them (perhaps interacting with other factors like SB time-budgets and the severity of any underlying  
537 brain dysfunction). Also, our data revealed that caged mink are highly sensitive to conspecific presence.  
538 This adds to past research showing that visually isolating female mink improves their reproductive  
539 success, an effect attributed to stress reduction (Gilbert & Bailey, 1967; although *cf.* Møller, 1991), and to  
540 past suggestions that mink modify their behaviour to avoid being active at the same time as their  
541 neighbours (De Jonge, Carlstead, & Wiepkema, 1986). Several decades and many captive generations  
542 later, farmed mink still seem averse to conspecific proximity, an effect that may typify naturally solitary  
543 Carnivora (Clauss, Müller, Steinmetz, & Hatt, 2010).

544  
545 Turning to future research, we recommend a replication of our studies using more animals and subjects  
546 pre-selected to have either only one SB subtype or an individual repertoire of several SB subtypes. This  
547 type of ideal sample could then be used to clarify whether individual mink with different SB subtypes  
548 correspondingly have diverse SB triggers or treatments, or whether it is the diverse SBs themselves (even  
549 *within* individuals) that differ. Greater differences may also emerge between head-only and whole-body

subtypes with more statistical power. Such future studies should also ensure observers are blind to hypotheses, and collect data throughout the day (to ensure that any treatment effects, especially on abolition, are consistent over time). Regarding the treatments themselves, they should ideally be more effective and distinct than the ones used here. Our neighbour removal manipulation was relatively mild because we removed only one of two neighbours for most subjects; while our enrichment-provision was confounded with reduced neighbour proximity (since distances between neighbours were approximately doubled by access to the enriched compartments). Treatments should also be more numerous, as using only two manipulations limited our ability to resolve differences between the three SB subtypes. Additional treatments might include delayed weaning, supplying chewing ropes, providing chunky or *ad libitum* food, or increasing total feed levels (*cf.* e.g., Hansen & Møller, 2008; Jeppesen, Heller, & Dalsgaard, 2000; Malmkvist, Palme, Svendsen, & Hansen, 2013; Mason, 1993, 1994). Lastly, to better understand the motivational basis and welfare implications of scrabbling, future mink studies should ascertain whether aggressive temperaments or high testosterone levels predict more neighbour-directed scrabbling in males, and whether conspecific proximity is particularly stressful for those individuals who scrabble or have scrabbling neighbours.

## ***Conclusions***

Our first two studies supported the hypotheses that scrabbling in mink reflects underlying motivations to interact with neighbouring conspecifics and can be reduced by removing neighbours, while our third study demonstrated that physical enrichment is a better treatment for head-only and whole-body SBs. Our results thus add to growing evidence that SBs are heterogeneous, with different subtypes having different triggers and being best tackled in different ways. Together, they emphasise the importance of identifying valid SB subcategories rather than pooling all SBs as if homogeneous. For Carnivora in zoos and conservation breeding centres, we therefore recommend that future attempts to treat SBs involve careful assessment of the degree to which each different form is reduced by each specific enrichment or

treatment. Doing so will assess whether heterogeneity effects like ours occur in other species and provide the knowledge essential for tailoring treatments to tackle SBs most effectively.

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