1   **Stereotypic behaviours are heterogeneous in their triggers and treatments in the American mink**

2   *(Neovison vison)* **— a model Carnivore**

3

4   Stereotypic behaviours (SBs) are common in confined animals including captive Carnivora. These display

5   diverse forms of SB: often whole-body movements (e.g., pacing), but also head-only movements (e.g.,

6   head-twirling) and "scrabbling" (scratching at enclosure boundaries). Although often pooled together,

7   emerging evidence indicates that SBs are heterogeneous, suggesting that subtypes differ in their causes,

8   triggers, and consequently treatments. In mink, a model Carnivore, scrabbling seems to be elicited by

9   neighbouring conspecifics. We tested this hypothesis *via* three studies of 32 males (individually-caged in

10   rows, and separated by solid partitions). Study 1 investigated whether neighbour proximity affects the

11   location of any SBs, and Study 2, whether removing neighbours reduces any SBs. Results revealed that

12   although mink typically avoided proximity to their neighbours, scrabbling was uniquely directed towards

13   neighbours who were close to the shared cage partition ($Z < 3.59$, $P < 0.05$). It was also the only SB

14   significantly elevated by having all-male neighbours, and reduced by removing neighbours ($Z < 2.75$, P

15   < 0.05). Study 3 then investigated whether environmental enrichment – a standard SB treatment – would

16   reduce or abolish different SBs equally, to assess whether scrabbling is simply easier to alleviate than

17   other SBs. Enrichment reduced all SB subtypes ($Z = 4.38$, $P < 0.05$), but logistic regressions revealed that

18   the odds of complete abolition were higher for whole-body ($OR < 10.09$, $P < 0.05$) and head-only SBs (OR

19   < 28.73, $P < 0.01$) than for scrabbling. Overall, these naturally solitary Carnivores thus seem to avoid

20   conspecific proximity, but they specifically direct their stereotypic scrabbling at neighbours; and their

21   scrabbling is reduced by neighbour-removal, while their whole-body and head-only SBs are instead better

22   alleviated with enrichment. Understanding that Carnivore SBs are heterogeneous in their triggers and

23   most effective treatments may help zoos, breeding centres and mink farms improve the design of their

24   enclosures and the efficacy of their enrichments.

25

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":

52   Hansen & Jeppesen, 2001; Morabito & Bashaw, 2012; Polanco, Campbell, Díez-León, & Mason, 2017).

53   We therefore used mink in a series of three experiments aimed at investigating the factors affecting these

54   different forms of Carnivora SB.

55   Since the 1960s, researchers have suggested that SBs are heterogeneous (e.g., Berkson, 1967;

56   Keiper, 1969; see also Mason, 1991, 1993; Mason & Turner, 1993). Emerging empirical evidence

57   supports this view: SBs vary in their links with other welfare indicators (e.g., Novak, Bailoo, Melotti, &

58   Würbel, 2016; Pomerantz, Paukner, & Terkel, 2012; Pomerantz, Terkel, Suomi, & Paukner, 2012); the

59   degree to which different environmental contexts enhance their development (Campbell, Dallaire, &

60   Mason, 2013; Gross, Engel, Richter, Garner, & Würbel, 2011; Jones, Mason, & Pillay, 2011; Tan et al.,

61   2013); their epidemiological risk factors in terms of both husbandry (Bashaw, Tarou, Maki, & Maple,

62   2001; Greco, Meehan, Heinsius, & Mench, 2017; Waters, Nicol, & French, 2002) and species-typical

63   behavioural biology (Kroshko et al., 2016; Pomerantz, Meiri, & Terkel, 2013); and finally, in whether

64   they are associated with generalised behavioural inflexibility (Kirsty, Andrew, Meriel, & Catherine, 2015;

65   Novak et al., 2016; Pomerantz, Paukner, et al., 2012). Despite this, most studies, including those of mink,

66   still pool SBs into one single, homogeneous category (e.g., Anderson, Arun, & Jensen, 2010; Hansen,

67   Møller, & Damgaard, 2011; Tilly, Dallaire, & Mason, 2010).

68   Recently, we found strong empirical evidence of SB heterogeneity in mink, with whole-body and

69   head-only SBs negatively correlating with each other and with scrabbling, potentially suggesting three

70   distinct subgroups with different causal bases (Polanco et al., 2017). This, in turn, suggests that diverse

71   methods might be best for reducing or preventing these different SB subtypes. If correct, such information

72   could help animal care personnel prevent and alleviate SBs more effectively in mink and other Carnivore

73   species. Indeed, despite previous studies examining SB triggers across different species (see Clubb &

74   Vickery, 2006 and Rose, Nash, & Riley, 2017 for reviews), no experiment to date has investigated the

75   triggers of different SBs within the same species. Furthermore, we know of only two experiments to

76   explicitly investigate the relative effectiveness of various environmental improvements on different forms

77   of SB, neither using pre-validated SB subtypes (instead categorising SBs informally by form). Keiper

78   (1969, 1970), working with canaries, found that route-tracing, but not stereotypic spot-picking, was

79   reduced by large aviary cages, swinging perches and group housing, while providing seed bells as

80   foraging enrichments uniquely reduced spot-picking. More recently, Malmkvist, Palme, Svendsen, &

81   Hansen (2013) found that biting ropes successfully reduced fur-chewing in mink, but not "locomotor"

82   SBs (a category pooling whole-body and head-only SBs), even though both SBs could be reduced by

83   supplying chunky feed. Here, we present three experiments that build on our previous work to investigate

84   whether: 1) different SB subtypes, already well-validated as distinct subgroups (Polanco et al., 2017),

85   differ in their environmental triggers, and 2) removing a neighbour and providing environmental

86   enrichment are equally or differentially effective at alleviating these different SBs.

87

STUDY 1: NEIGHBOUR PROXIMITY

89   One hypothesised underlying basis or trigger for some SBs is the frustration of motivations to reach

90   resources or other animals outside of the cage. For instance, elegant experiments on laboratory mice have

91   shown that bar-related SBs (e.g., bar-chewing and -sniffing) derive from motivations to escape the cage

92   and/or investigate environmental cues outside it (Nevison, Hurst, & Barnard, 1999, Lewis & Hurst,

93   2004). Likewise, in several Carnivores, SBs can occur at boundaries separating subjects from feeding

94   areas (Cless & Lukas, 2017) or conspecifics (Clubb & Vickery, 2006; Vickery & Mason, 2004). For

95   instance, some farmed silver fox *(Vulpes vulpes)* and blue fox *(Alopex lagopus)* SBs are performed in

96   parallel with those of foxes in neighbouring cages (European Commission, 2001). Likewise, pacing

97   occurs against fences separating adult conspecifics from each other in cheetahs (*Acinonyx jubatus:* Lyons,

98   Young, & Deag, 1997) and dingoes *(Canis lupus dingo:* Meyer-Holzapfel, 1968). In mink, males may

99   direct SBs towards reproductively-receptive neighbouring females (along the shared cage wall), while

100   mink mothers separated from their offspring may show SBs against the intervening barrier (Mason,

101   1993); and scrabbling appears particularly likely to be directed towards neighbouring animals or

102   inaccessible cage areas (Dallaire, 2011; Hansen & Jeppesen, 2000). Such observations suggest that some

103   Carnivore SBs represent thwarted motivations to approach conspecifics or resources, but no experiments

104 have tested this hypothesis. We therefore assessed whether any subtypes of SB represent frustrated

105 attempts to reach neighbouring conspecifics. In this first study, we investigated the effects of neighbour

106 number and sex on male minks' SB time-budgets. We also recorded where their SBs were performed, to

107 assess whether the locations of any subtypes were indeed affected by neighbour proximity. If previous

108 observations were correct, scrabbling should be particularly likely to be directed towards neighbours.

109

110 ***Methods***

111 All three studies received ethical approval from the University of Guelph's Animal Care Committee

112 (AUP 3246) and Michigan State University's Institutional Animal Care and Use Committee (AUF 12/14-

113 226-00).

114

115 *Subjects and housing*

116 Subjects were 32 unrelated male mink housed at Michigan State University's Experimental Fur Farm

117 (though halfway through the study when subjects were 10 months old, one mink was assigned to another

118 project reducing the N to 31). They were individually-housed (as standard for this species) in rows of

119 cages (W60cm x L75cm x H45cm) primarily made of wire-mesh, but with side walls of opaque plastic (c.

120 3mm thick). Each cage had an exterior nestbox (W25cm x L25cm x H30 cm) and some enrichment (i.e., a

121 shelf-like structure and a wiffle ball) to comply with Canadian Codes of Practice (National Farm Animal

122 Care Council, 2013). Due to the facility's layout, subjects were caged either between two male

123 neighbours (n = 12), between one female and one male (n = 12), or — if at the end of a row — beside one

124 male (n = 4) or one female (n = 4) of the same age and colour type. Thus, 28 subjects had at least one

125 male neighbour, while 16 had one female neighbour. Their cages' opaque plastic side walls meant they

126 could hear and smell their neighbours, but not see them. Figure 1 gives a timeline of the three

127 experiments.
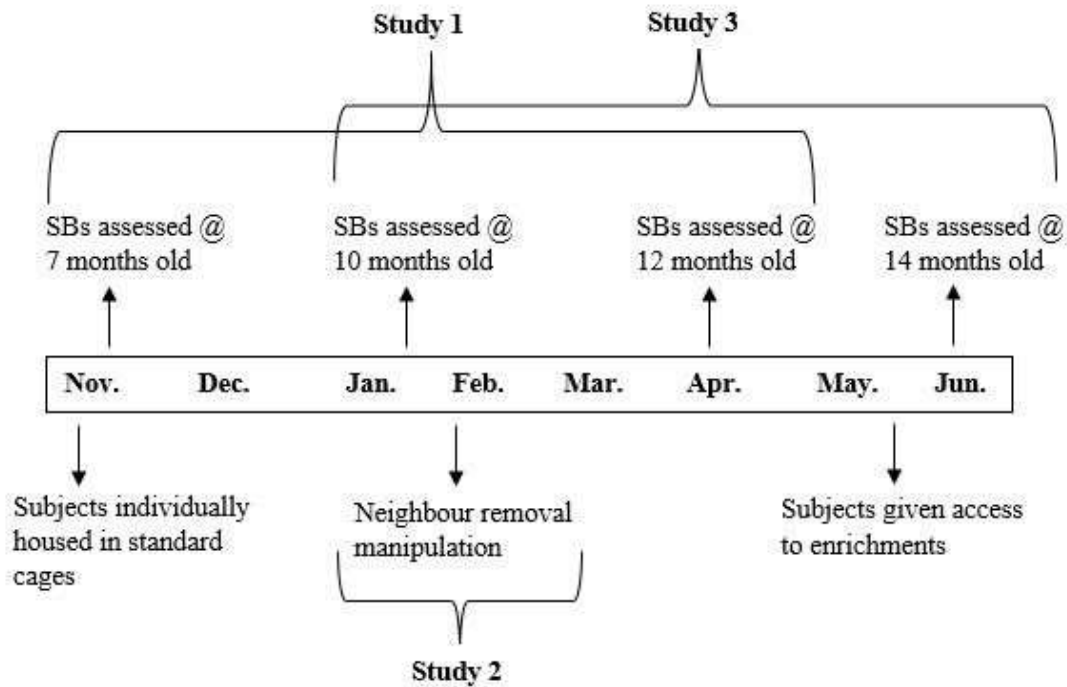
Figure 1. Timeline for the three studies

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

6

142 recorded). Subjects were scored as being close to neighbours if immediately adjacent to the neighbour at

143 the time of the scan (e.g., if the subject was in the southwest quadrant of his cage and the corresponding

144 neighbour was in the southeast quadrant of his/her cage; Figure 2). If the subject was in the centre of his

145 home cage (a rare occurrence) or inside his nestbox, these observations were excluded because we were

146 only interested in home cage behaviour that could unambiguously be scored as close to or far from a
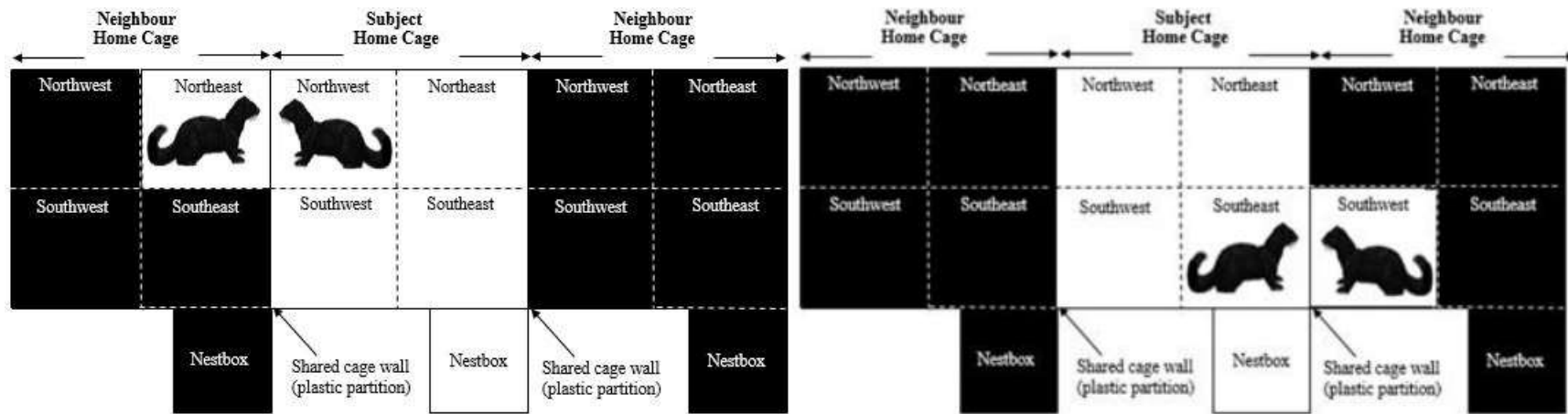
147 neighbour.

148

Behaviour		Description
Stereotypic behaviours	Head-related SBs	Head-only movements, including head-bobbing, head-twirling and head-weaving, repeated at least three times within a bout
	Whole-body SBs	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

149

150 **Table 1. Ethogram used**

151 **1)**   **2)**

152

153

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

Neighbours were "close" if immediately adjacent to the subject, for example, if the subject was "northwest" and the neighbour "northeast" (1), or

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

in the areas shaded in black.

158 *Statistical analyses*

159 Data were analysed with STATA 14.2 (StataCorp, College Station, TX) and JMP 12 (SAS Institute, Cary,

160 NC). Non-parametric tests were used as the data could not be transformed to meet parametric

161 assumptions of homogeneity of variance. Because SB time-budgets are generally consistent from 10 to 12

162 months of age (Polanco et al., 2017), and since there were not enough data to analyse 10 and 12 months

163 of age separately, we pooled data from these ages (young adulthood); but we analysed data from 7

164 months of age (adolescence) separately.

165

166 Before testing our hypothesis, we assessed baseline behaviour to generate descriptive statistics (e.g., the

167 prevalence and average time-budgets of each SB subtype) and evaluate whether time-budgets differed

168 between SB subtypes using Wilcoxon signed-rank tests. Further, we investigated whether baseline SB

169 differed between mink with only male neighbours (versus also a female), or two neighbours (versus one),

170 *via* Wilcoxon rank-sum tests. Additionally, to check whether any effects were specific to SBs *per se,* we

171 assessed whether neighbour sex and the number of neighbours influenced normal activity.

172

173 To test our hypothesis about SB location, we calculated the proportion of each SB subtype occurring in a

174 quadrant scored as "close to neighbour" (i.e., observations of that SB subtype performed close to a

175 neighbour/total observations of that SB subtype). Additionally, we assessed whether neighbour proximity

176 affected the proportion of normal activity performed close by in the home cage. Because each quadrant

177 was ¼ of the home cage, the probability of a subject and neighbour being in adjacent quadrants if moving

178 at random was 0.125 (2*[0.25*0.25]). Thus the null hypothesis was that subjects would allocate 12.5% of

179 each behaviour to a quadrant close to a neighbour, with significantly greater proportions indicating a

180 preferential use of such quadrants. The proportions of each behaviour located "close to neighbour" were

181 therefore compared to 0.125, using one-sample Wilcoxon signed-rank tests. Separate Wilcoxons were

182 also run based on the sex of the neighbour, here and in the subsequent study, as initial results suggested

183 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 ≥ 0.05 and ≤ 0.10.

189

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 ($Z = 0.33$, $P = 0.75$).

202

203

Descriptive Statistic	SB subtype		
Prevalence of SB[1]	Scrabble	Head-only	Whole-body
7 months old	94%	19%	19%
10-12 months old	84%	32%	32%
Median and IQR (% of observations)			
7 months old	5% (2-7%)	0 (0%)	0 (0%)
Only mink with that subtype	*5% (2-7%)[2]*	*5% (1-8%)[3]*	*2% (0.7-2%)[3]*
10-12 months old	4% (3-9%)	0 (0-2%)	0 (0-0.3%)
Only mink with that subtype	*5% (3-9%)[4]*	*2% (2-5%)[5]*	*2% (0.3-4%)[5]*

[1] *based on entire sample size (7 months old: n = 32; 10-12 months old: n = 31)*

[2] *n = 30*

[3] *n = 6*

[4] *n = 26*

[5] *n = 10*

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

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

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

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

231 The proportion of normal activity performed close to female neighbours was not significantly different

232 from chance when mink were adolescent, but tended to be lower than chance in adulthood. Likewise, this

233 class of behaviour was significantly unlikely to occur near male neighbours when subjects were adults:

234 only 4% of all normal activity occurred in a quadrant near a male neighbour at 10-12 months of age

235 (Table 3).

236

237 The proportion of scrabbling located close to a neighbour was, in contrast, significantly higher than

238 chance, with 50-89% being performed in cage quadrants close to a neighbouring conspecific (see Table

239 3). The location of head-only SBs was not significantly affected by neighbour proximity; however,

240 whole-body SBs were significantly likely to be located away from neighbours in older mink (the *n* being

241 too small for analysis when mink were younger).

242

243 These effects were preserved in *post hoc* exploratory analyses on the subset of individuals who performed

244 more than one SB subtype ($n = 13$), such that scrabbling was still directed towards neighbours ($Z < 2.28$, P

245 <0.05) while other SB forms were either still not significantly influenced by neighbours (head-only SBs:

246 $Z < -0.69$, $P > 0.10$) or directed away from neighbours (whole-body SBs: $Z < -2.25$, $P < 0.05$).

247

A) Effects of male neighbour proximity

	7 months old				10-12 months old			
	n	Median proportion performed in quadrant "close to neighbour" (+ interquartile range)	z test statistic	P value	n	Median proportion performed in quadrant "close to neighbour" (+ interquartile range)	z test statistic	P value
Normal Activity	28	0.06 (0.01-0.17)	-1.62	0.11	28	0.04 (0-0.14)	-2.11	**0.035**
Scrabble	20	0.66 (0.29-1)	3.58	**0.0003**	21	0.75 (0.17-1)	3.35	**0.0008**
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[1]	-----	-----	-----	6	0 (0-0)	-2.45	**0.01**

B) Effects of female neighbour proximity

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

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

Significant or trending p-values are shown in bold.

[1] *n too small for analysis*

255 **Table 3. The proportions of normal activity and each SB subtype performed in cage quadrants**

256 **close to male or female neighbours, compared to chance levels (0.125) using one-sample Wilcoxon**

257 **signed-rank tests**

258

259 **STUDY 2: NEIGHBOUR REMOVAL EXPERIMENT**

260 In addition to observational studies reporting *where* SBs occur, some research has investigated whether

261 SB time-budgets are affected by neighbour proximity. In naturally solitary species like the okapi (*Okapia*

262 *johnstoni*), head-rolling is higher when there is visual access to conspecifics (Troxell-Smith and Miller,

263 2016). Likewise in the Carnivora, pacing is often higher in naturally solitary species that can view

264 conspecifics (e.g., cheetahs *[Acinonyx jubatus]*: Quirke et al., 2012; tigers *[Panthera tigris]*: Rouck et al.,

265 2005), but is lowered by visual barriers (e.g., tigers: Miller, Bettinger, & Mellen, 2008). However, SBs

266 can also increase when conspecifics are out of sight (e.g., in polar bears *[Ursus maritimus]*: Kelly et al.,

267 2015) or when visually isolated from each other (*via* opaque barriers; e.g., tigers: Bashaw et al., 2007).

268 These contradictory findings could reflect many factors, including the sex of the subjects and their

269 neighbours, that visual isolation does not ensure complete sensory isolation from conspecifics, and

270 individual differences in the SB subtypes performed. In mink, if neighbour proximity truly triggers

271 scrabbling, as indicated by Study 1, then experimentally removing neighbours should reduce this SB

272 subtype.

273

274 *Methods*

275 Subjects and housing were as in Study 1, but all animals were 10 months old when these data were

276 collected. To investigate effects of neighbour presence on subject behaviour, we removed one neighbour

277 per subject by giving him or her voluntary access to an enriched compartment (as described in the next

278 study), into which this animal was then locked for approximately 4 hours (from 08:00 h to 12:00 h) on

279 one day. In total, we removed 15 female and 16 male neighbours. For the 24 mink with two neighbours,

280 we removed only one because only half of the facility's cages had access to an enriched compartment.

14

281 *Behavioural Observations*

282 We collected baseline behavioural data (*cf.* Table 1) during one 6-day period when mink were 10 months

283 old (as in Study 1) from 08:00 h to 12:00 h. We conducted the neighbour removal manipulation two days

284 later using the same data collection methods as Study 1 (i.e., observations occurred from 08:00 h to 12:00

285 h over the course of one morning). Behaviours in the nestbox were excluded from analyses to be

286 consistent with Study 1.

287

288 *Statistical Analyses*

289 Again, data were analysed with STATA 14.2 (StataCorp, College Station, TX), using non-parametric

290 tests since parametric assumptions were unmet. To test our prediction that scrabbling would be the only

291 behaviour affected by the manipulation, we used Wilcoxon signed-rank tests to compare the time-budgets

292 of each SB subtype (i.e., observations of SB subtype/total number of observations) pre- and post-

293 neighbour removal, split by the sex of the removed neighbour. Again, we conducted *post hoc* analyses

294 focusing on the subset of 13 individuals who performed more than one SB subtype. As a control, we also

295 assessed whether the time spent performing normal activity (i.e., observations of all normal

296 behaviours/total number of observations) was affected by the manipulation.

297

298 To evaluate the efficacy of removing a neighbour as a treatment for SB, we ran a mixed logistic

299 regression to see whether SB subtype predicted SB abolishment post-treatment (yes/no) with "yes"

300 indicating that performance of the SB ceased post-treatment (at least during the pre-feed period assessed)

301 and "no" indicating continued performance (even if at reduced levels). We included mink ID as a random

302 effect and neighbour sex as a blocking factor. Homoscedasticity and normality of the best linear unbiased

303 predictions (BLUPs) were assessed graphically.

304

305 **Results**

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

15

307   Removing both male and female neighbours significantly reduced the time spent scrabbling. Removing

308   female neighbours tended to reduce head-only SBs. Whole-body SBs appeared unaffected by the

309   manipulation (see Table 4). However, the same patterns could not be detected in the 13 mink with more

310   than one SB subtype ($Z <1.22$; $P >0.10$), although this may reflect low power. The time spent performing

311   normal behaviours also appeared unaffected by removing a neighbour (Table 4).

312

	Male Neighbours				Female Neighbours			
	n	Median (+ interquartile range)	z test statistic	P value	n	Median (+ interquartile range)	z test statistic	P 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	**0.006**	10	Baseline 0.04 (0.03-0.07) Removed 0.03 (0-0.03)	2.09	**0.04**
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	**0.07**
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

313   *Note: Numbers differ between analyses as mink not performing each behaviour type during baseline were*

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

315   **Table 4. Wilcoxon signed-rank tests comparing normal activity and each SB subtype as proportions**

316   **of observations when male and female neighbours were in their home cages *versus* "removed"**

317

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

319   Within the subjects performing each particular SB subtype, 46% of scrabblers stopped performing this

320   subtype after neighbour removal; 60% of mink with head-only SBs stopped performing this subtype; and

321   44% of subjects with whole-body SBs stopped performing this subtype. However, the mixed logistic

322   regression revealed no significant effect of SB subtype on the odds of abolition ($x^2 [2] = 0.28$, $P = 0.87$).

323 Furthermore, the sex of the removed neighbour had no significant effect on the odds of SB abolition

324 ($x^2[1] = 0.51$, $P = 0.47$). Table 5 gives details.

325

Variable	B	SE	Odds Ratio	95% CI for Odds Ratio	P
SB Subtype:					
Scrabble (referent)					
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:					
Female (referent)					
Male	-0.81	1.13	0.45	0.05-4.07	0.47

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

327 **Table 5. Mixed logistic regression model assessing predictors of SB abolition during the neighbour-**

328 **removal treatment ($n = 28$)**

329

330 **STUDY 3: EFFECTS OF ENVIRONMENTAL ENRICHMENT**

331 Previous research has shown that head-only and whole-body SBs (pooled into one category) and

332 scrabbling are both reduced if mink are raised in large enriched enclosures. However, only the former

333 remain low if enriched-raised mink are transferred to small barren cages while scrabbling instead

334 increases (Díez-León et al., 2016). Moreover, high levels of head-only and whole-body SBs (pooled)

335 predict poor mating success in males, while scrabbling does not (Díez-León et al., 2013). Together, this

336 led us to hypothesise that head-only and whole-body SBs reflect long-term alterations in behavioural

337 organisation, perhaps mediated by changes in brain function (*cf.* Lewis, 2004), but that scrabbling reflects

338 more readily reversible effects of motivational frustration (Díez-León et al., 2016). If correct, scrabbling

339 would be easier to treat than head-only and whole-body SBs (i.e., declining to low levels at faster rates

340 whenever conditions improve), as it would not be a product of long-term neurological changes. This view

341 provides an alternative explanation for Study 2's results: that they do not indicate a specific effect of

342 neighbours on scrabbling, but instead merely that this SB subtype is more labile than others.

343 To investigate this possibility, we gave our subjects a standard SB treatment, environmental enrichment

344 (EE). EE comprises sensory, cognitive, physical, and/or manipulable stimuli meant to improve captive

345 animals' welfare (e.g., Swaisgood & Shepherdson, 2005). We used enriched compartments previously

346 shown (albeit in a modified form, see Methods below) to reduce the development of all SB subtypes in

347 mink (e.g., Campbell et al., 2013; Dallaire et al., 2012; Díez-León et al., 2013, 2016; Hansen et al., 2007;

348 Meagher & Mason, 2012; Meagher et al., 2013) and to be highly preferred (mink being willing to pay

349 costs to access such enrichments: Dallaire et al., 2012; Mason, Cooper, & Clarebrough, 2001). The

350 primary purpose of this last experiment was to assess whether different SB subtypes vary in the degree to

351 which EE reduces or even abolishes them. If EE had a greater effect on scrabbling than on head-only and

352 whole-body forms, then this would suggest that Study 2's results did not reflect a specific effect of

353 conspecific proximity, but instead were just a by-product of scrabbling being easier to alleviate.

354 Opportunistically, this study also allowed us to test a second hypothesis. One previous mink study found

355 that a reduction in head-only and whole-body SBs (pooled) in enriched housing was predicted not by

356 active enrichment use, but instead by the previously highly-stereotypic individuals spending more time

357 resting in the towers and tunnels of their new enclosures (Dallaire et al., 2012). Inspired by this, we

358 therefore collected subsidiary data on our minks' enrichment use and resting behaviour after transfer to

359 enriched cages to see if either predicted how successfully EE reduced any of the three SB subtypes.

360

361 ***Methods***

362 The same subjects were given access to enriched compartments (as also used to remove neighbours in

363 Study 2) when 14 months old. Their layouts were as described in prior research (e.g., Dallaire et al., 2012

364 and Díez-León et al., 2013), although the contents differed. In this study, a tunnel connected to the

365 standard cage could be opened, giving subjects access to climbing opportunities, an elevated tunnel with

366 an aerial view of the facility, and a large enriched compartment containing manipulable toys (e.g.,

367 hanging ropes/towels, plastic toys, and brushes) and shelf-like structures (e.g., wire-mesh 'tunnels' and a

368 plastic toy bucket that the mink typically lay in). However, unlike prior research using the same facility,

369   we did not provide channels of running water for mink to swim in. Half of the mink ($n = 15$) were given

370   access to these resources earlier in another study, while the remainder ($n = 16$) were given access 13 days

371   later. Regardless, each enriched compartment was consistent across subjects and throughout the study.

372

373   *Behavioural observations*

374   While mink were still in their standard cages, we collected behavioural data (*cf.* Table 1) throughout two

375   6-day periods at 10 and 12 months (from 08:00 h to 12:00 h), subsequently pooled for analyses (as in

376   Study 1). After subjects were given access to enriched housing, we collected data again during an 8-day

377   period from 08:00 h to 12:00 h, using the same methods as before but additionally recording presence in

378   enriched housing (i.e., any time spent in the enriched areas, including the towers and tunnel), enrichment

379   manipulation (i.e., any interaction with enrichment items), and inactivity in the towers/tunnels. To be

380   consistent with the prior two studies, behaviours in the nestbox were excluded.

381

382   *Statistical analyses*

383   Data were again analysed with STATA 14.2 (StataCorp, College Station, TX) and unless otherwise

384   stated, non-parametric tests were used. One subject never entered his enriched enclosure and was

385   therefore excluded from analyses. Our first objective was to investigate whether EE differentially affected

386   the different SB subtypes. Here we used Wilcoxon signed-rank tests to compare the time-budgets of each

387   SB subtype (i.e., observations of SB subtype/total number of observations) pre- and post-EE (also

388   assessing whether the time spent performing normal activity was affected by EE). Like Study 2, we

389   additionally ran a mixed logistic regression to see whether a SB's subtype predicted whether it would be

390   abolished by EE (yes/no) with "yes" indicating that performance of the SB ceased post-treatment (at least

391   during the pre-feed period assessed) and "no" indicating that it continued (even if at reduced levels). We

392   included mink ID as a random effect and EE access time (early/later) as a blocking factor. We ran an

393   additional logistic model with time spent stereotyping in standard housing as a covariate to see whether

394   any effect of SB subtype in the first model remained significant, since baseline SB time-budgets differed

395 by subtype (see Study 1) and this could have explained our first model outputs. Again, we assessed

396 homoscedasticity and normality of the BLUPs graphically and conducted *post hoc* analyses on the subset

397 of 13 individuals who performed more than one SB subtype.

398

399 Our second objective was to investigate whether the subtype of baseline SB predicted how mink utilised

400 their new enclosure, to potentially replicate and extend Dallaire and colleagues' (2012) findings. To do

401 this, we ran Spearman correlations between the time-budgets of each SB subtype pre-EE and the

402 following behaviours post-EE: inactivity in the towers/tunnels, presence in enriched housing, and

403 enrichment manipulation. Additionally, classifying subjects by their most common (i.e., time-consuming)

404 SB during baseline, we ran Kruskal-Wallis tests to investigate whether such mink differed in their

405 utilisation of the new resources and enrichment behaviours.

406

407 ***Results***

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

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

410 tended to increase.

411

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

412 *Note: Numbers differ between analyses as mink not performing each behaviour type during baseline were*

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

414 **Table 6. Wilcoxon signed-rank tests comparing time-budgets of normal activity and each SB**

415 **subtype in non-enriched (NE) conditions *versus* when given environmental enrichment (EE)**

416

417 *Effect of SB subtype on SB abolition by enrichment*

418 31% of scrabblers ceased performing this subtype after enrichment-provision, as did 80% of mink with

419 head-only SBs and 70% of mink with whole-body SBs; and the mixed logistic regression revealed a

420 significant effect of SB subtype on the odds of abolition by EE (x^2 *[2] =* 16.34, *P* = 0.003), this being

421 significantly higher for head-only and whole-body SBs than for scrabbling. This result held even after

422 controlling for time spent stereotyping in non-enriched housing (which also had a significant,

423 independent effect: $x^2[1]$ *=* 9.93, *P* = 0.0016). The 13-day difference in enriched access had no significant

424 effect in either model ($x^2[1]$ *<*1.52, *P* >0.10). Table 7 gives details. As in Study 2, the effects of SB

425 subtype became non-significant when focussing only on the 13 mink with more than one SB subtype (x^2

426 *[2]* <3.13, *P* >0.10).

427

A)

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

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

B)

Variable	*B*	SE	Odds Ratio	95% CI for Odds Ratio	*P*
SB Subtype:					
Scrabble (referent)					
Head-only SBs	3.36	1.23	28.72	2.59-318.05	**0.006**
Whole-body SBs	2.31	0.95	10.08	1.57-64.68	**0.015**
EE Access:					
Early (referent)					
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	**0.002**

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

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 ($n = 28$)

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

442   We found no significant relationships between pre-EE levels of SB and the time spent in any of the

443   enriched areas or actively using enrichments. However, there was an unexpected significant negative

444   correlation between pre-EE levels of head-only SBs and the time spent inactive in the towers and tunnels

445   (see Table 8). Likewise, there were no significant differences between mink favouring the three SB

446   subtypes in the time they spent in enriched housing (x^2 [2] = 1.41, P = 0.49), using enrichments (x^2 [2] =

447   1.69, P = 0.43), or showing inactivity in the towers and tunnels (x^2 [2] = 0.003, P = 0.99).

448

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

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

461   *excluded.*

462   **P <0.05*

463
464   **Table 8. Spearman correlations for time-budgets of baseline SB subtypes and behaviours when**

465   **given EE**

466

467   **GENERAL DISCUSSION**

468   Our results demonstrate that Carnivora SBs are heterogeneous in both their triggers and their most

469   effective treatments. They also show that caged male mink are sensitive to neighbour effects, and provide

470   new insights into what makes some SBs more 'treatable' than others. Here, we discuss these findings'

471   implications for the welfare of mink and other Carnivora and outline key future research directions.

23

472   Given its unequivocal results, we first consider our findings on scrabbling: the SB in which mink scratch

473   or dig at cage walls with their forepaws.

474

475   Scrabbling was the SB subtype displayed to the greatest extent by mink with all-male neighbours, and the

476   only SB subtype to be significantly reduced by removing any type of neighbour. It was also uniquely

477   directed towards active, nearby conspecifics in terms of its location within the cage. In this regard, mink

478   seem to differ from other Carnivore species, which generally show pacing when displaying SB towards

479   inaccessible conspecifics (e.g., Lyons, Young, & Deag, 1997; Meyer-Holzapfel, 1968). However, this

480   may reflect scrabbling being quite uncommon in other Carnivora. Speculatively, scrabbling might perhaps

481   be restricted to those species which naturally dig, such as other mustelids (e.g., otters: Morabito &

482   Bashaw, 2012) and foxes (Korhonen & Huuki, 2011). In our subjects, scrabbling was also the SB subtype

483   least likely to be abolished by EE: a result consistent with long-term differentially housed mink, in which

484   EE was less effective at reducing scrabbling than whole-body and head SBs pooled (Campbell et al.,

485   2013). This demonstrates that scrabbling is not merely more sensitive to housing changes than other SB

486   subtypes (*cf.* Díez-León et al., 2016), and that its marked reduction in Study 2 did specifically reflect a

487   role of strong motivations to interact with neighbouring animals. In terms of precisely what these strong

488   motivations to interact represent, more research is needed (see below). However, we suspect that these

489   motivations are not playful, because play in 10-12-month-old mink is rare (Ahloy Dallaire & Mason,

490   2016; Hansen et al., 1997); instead, we hypothesise that they are agonistic, as aggression in mink often

491   develops around 5-6 months of age (Hansen, 1996) and sub-adult and adult males naturally compete over

492   territory in the wild (Dunstone, 1993).

493

494   Turning to whole-body SBs, like normal activity this type of behaviour was performed in locations away

495   from neighbours. However, avoiding conspecifics did not seem to be their primary underlying motivation:

496   their time-budgets were not significantly affected by neighbour sex or number and experimentally

497   removing neighbours did not reduce them. Instead, EE readily abolished these SBs: 7 of the 10 affected

498   subjects ceased to show them in our post-enrichment observations. Such whole-body SBs are typical for

499   captive Carnivora, although they were the least prevalent and time-consuming SB subtype in our mink.

500   Moreover across Carnivora, the time-budgets of route-tracing – the most common whole-body SB – are

501   systematically highest in species with large annual home ranges (Clubb & Mason, 2003, 2007; Kroshko et

502   al., 2016). This helps explain their low levels in mink (a species with naturally small home ranges), and

503   also suggests that they may derive from the location-shifting normally shown when resources are locally

504   suboptimal (a behaviour most marked in wide-ranging species: Clubb & Mason, 2007). That mink in our

505   study could move freely between the standard and enriched cage could perhaps mimic this natural degree

506   of choice, with this then contributing to SB reduction and, in some mink, abolition.

507

508   Lastly, we discuss our findings for head-only SBs. The time-budgets of this subtype were not affected by

509   neighbour sex, number, and presence, nor were their locations affected by neighbour proximity.

510   Removing a female neighbour tended to reduce them, but we suspect this to be a Type I error because

511   removing male neighbours had no similar effect, and there was no other evidence of neighbour effects.

512   Head-only SBs were instead similar to whole-body SBs in being more likely than scrabbling to be

513   abolished by EE in Study 3. However, it is unclear from where head-only movements derive. In rhesus

514   macaques, head-twirling and head-tossing (but not whole-body SBs) positively covary with behavioural

515   inflexibility in extinction tasks, potentially suggesting brain dysfunction (Pomerantz, Paukner, et al.,

516   2012). However, our attempts to replicate such findings in mink (using a different test) were not

517   successful (Polanco, 2016). Below we suggest some future research that may help clarify the aetiology of

518   these movements.

519

520   Together, these findings provide the first demonstration for *a priori* validated SB subtypes that distinct

521   forms are both differentially triggered by stimuli like conspecifics, and also variable in the treatments

522   most likely to reduce or abolish them. Furthermore, in our *post hoc* exploratory analyses of the subset of

523   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

550   subtypes with more statistical power. Such future studies should also ensure observers are blind to

551   hypotheses, and collect data throughout the day (to ensure that any treatment effects, especially on

552   abolition, are consistent over time). Regarding the treatments themselves, they should ideally be more

553   effective and distinct than the ones used here. Our neighbour removal manipulation was relatively mild

554   because we removed only one of two neighbours for most subjects; while our enrichment-provision was

555   confounded with reduced neighbour proximity (since distances between neighbours were approximately

556   doubled by access to the enriched compartments). Treatments should also be more numerous, as using

557   only two manipulations limited our ability to resolve differences between the three SB subtypes.

558   Additional treatments might include delayed weaning, supplying chewing ropes, providing chunky or *ad*

559   *libitum* food, or increasing total feed levels (*cf.* e.g., Hansen & Møller, 2008; Jeppesen, Heller, &

560   Dalsgaard, 2000; Malmkvist, Palme, Svendsen, & Hansen, 2013; Mason, 1993, 1994). Lastly, to better

561   understand the motivational basis and welfare implications of scrabbling, future mink studies should

562   ascertain whether aggressive temperaments or high testosterone levels predict more neighbour-directed

563   scrabbling in males, and whether conspecific proximity is particularly stressful for those individuals who

564   scrabble or have scrabbling neighbours.

565

566   ***Conclusions***

567   Our first two studies supported the hypotheses that scrabbling in mink reflects underlying motivations to

568   interact with neighbouring conspecifics and can be reduced by removing neighbours, while our third

569   study demonstrated that physical enrichment is a better treatment for head-only and whole-body SBs. Our

570   results thus add to growing evidence that SBs are heterogeneous, with different subtypes having different

571   triggers and being best tackled in different ways. Together, they emphasise the importance of identifying

572   valid SB subcategories rather than pooling all SBs as if homogeneous. For Carnivora in zoos and

573   conservation breeding centres, we therefore recommend that future attempts to treat SBs involve careful

574   assessment of the degree to which each different form is reduced by each specific enrichment or

575   treatment. Doing so will assess whether heterogeneity effects like ours occur in other species and provide

576   the knowledge essential for tailoring treatments to tackle SBs most effectively.

577

584

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