

Aberystwyth University

Causal factors or oral versus locomotor stereotype in the horse

Roberts, Kirsty; Hemmings, Andrew ; McBride, Sebastian; Parker, Matthew

Published in:

Journal of Veterinary Behavior: Clinical Applications and Research

DOI:

[10.1016/j.jveb.2017.05.003](https://doi.org/10.1016/j.jveb.2017.05.003)

Publication date:

2017

Citation for published version (APA):

Roberts, K., Hemmings, A., McBride, S., & Parker, M. (2017). Causal factors or oral versus locomotor stereotype in the horse. *Journal of Veterinary Behavior: Clinical Applications and Research*, 20, 37-43.
<https://doi.org/10.1016/j.jveb.2017.05.003>

Document License

CC BY-NC-ND

General rights

Copyright and moral rights for the publications made accessible in the Aberystwyth Research Portal (the Institutional Repository) are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the Aberystwyth Research Portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the Aberystwyth Research Portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

tel: +44 1970 62 2400
email: is@aber.ac.uk

1 Causal Factors of Oral versus Locomotor Stereotypy in the Horse

2
3 Kirsty Roberts¹, Andrew J. Hemmings¹, Sebastian D. McBride², & Matthew O.
4 Parker³

5 ¹Royal Agricultural University, Stroud Road, Cirencester, Gloucestershire, GL7
6 6JS

7
8 ²Aberystwyth University, Penglais, Aberystwyth, Ceredigion, SY23 3DA

9
10 ³School of Health Sciences and Social Work, University of Portsmouth, James
11 Watson West building, 2 King Richard 1st Road, Portsmouth, Hampshire, PO1
12 2FR

13
14 Corresponding Author: K. Roberts Tel: 01285 652531.
15 kirsty.roberts@student.rau.ac.uk

16
17 Abstract

18 Stereotypic behaviours are commonly observed in domestic equids, as they are in
19 a range of captive, non-domesticated species. Estimates suggest that 19.5-
20 32.5% of horses perform a stereotypy. The presence of these behaviours is
21 thought to indicate sub-optimal welfare status, and can result in secondary
22 physical pathologies such as colic, ligament strain and incisor wear. Relatively
23 little is understood about the aetiologies of oral and locomotor stereotypies.
24 Seemingly disparate causal factors have been proposed including gastric
25 pathology, neural adaption and genetic predisposition. In this review we propose a

26 model of causality which presents separate pathways to the development and
27 continuation of oral behaviours such as crib-biting, compared to locomotor
28 alternatives (i.e., weaving). The word 'stereotypy' has alarmingly negative
29 connotation among horse keepers. Stereotypic behaviours are often viewed as
30 'vices' and so a number of horse owners and establishments attempt to physically
31 prevent the behaviour with harsh mechanical devices. Such interventions can
32 result in chronic stress, and be further detrimental to equine welfare. Stereotypy
33 has been proposed to be a stress coping mechanism. However, firm evidence of
34 coping function has proven elusive. Stereotypy a range of serious welfare issues
35 remain. This review will explore management options directed at both prophylaxis
36 and remediation.

37 **Keywords: crib-biting; weaving; striatum; dopamine.**

38 Introduction to Equine Stereotypy

39 Stereotypic behaviours are repetitive, invariant (Pell and McGreevy, 1999;
40 McBride and Hemmings, 2005; Ninomiya et al., 2007), idiosyncratic (Parker et al.,
41 2009) and induced by motivational frustration (Mason, 2006), repeated attempts to
42 cope or central nervous system dysfunction (McBride and Hemmings, 2009;
43 McBride and Parker, 2015). Crib-biting is an oral stereotypy, in which the animal
44 grasps a surface at chest height with the incisors, pulling back creating an arch
45 with the neck (Moeller et al., 2008; McBride and Hemmings, 2009; Wickens and
46 Heleski, 2010) accompanied by the sucking of air into the proximal oesophageal
47 region, creating an audible grunting sound (Nicol et al., 2002; Moeller et al., 2008;
48 McBride and Hemmings, 2009; Wickens and Heleski, 2010). Weaving is a
49 locomotor stereotypy, defined as the repetitive weight shift from one forelimb to
50 the other, often combined with lateral swaying of the head (Cooper et al., 2000;
51 McBride and Hemmings, 2005). Box-walking, also a locomotor stereotypic
52 behaviour, is the repetitive circular walking of the stable (McBride and Hemmings,
53 2009).

54

55 The extent of stereotypy manifestation would appear to differ between studies
56 dependant upon factors such as stereotypy type, breed and performance
57 discipline. For example, utilising a questionnaire based methodology McGreevy et

58 al. (1995) reported that the prevalence of stereotypy ranged from 19.5% to 32.5%
59 in horses from dressage, eventing and endurance backgrounds. A previous
60 review calculated that 4.3% of horses perform the oral stereotypy, crib-biting,
61 compared to 3.25% and 2.2%, respectively of horses that perform the locomotor
62 stereotypies weaving and box-walking based upon previous published study (see
63 McBride and Hemmings, 2009). Direct observations indicate that questionnaire-
64 based estimates of stereotypy may be conservative (Cooper et al., 2000).
65 Furthermore, certain breeds are more susceptible to stereotypy than others,
66 indicating a genetic component to the development of these behaviours in the
67 horse (Bachmann et al., 2003a; Albright et al., 2009; Wickens and Heleski, 2010).
68 Thoroughbred horses are thought to be 3.1 times (Bachmann et al., 2003a), and
69 warmbloods 1.8 times (Wickens and Heleski, 2010), more likely to perform crib-
70 biting behaviour than other breeds. The thoroughbred is also thought to be more
71 at risk of performing weaving behaviour (Ninomiya et al., 2007). It could be
72 argued, however that thoroughbred and warmblood horses are utilised more
73 greatly in performance disciplines, and that the increase prevalence of stereotypy
74 observed in these breeds is a manifestation of their more intense management
75 regimes.

76 Other abnormal behaviours of the horse which by some are considered
77 stereotypic include oral behaviours such as tongue-flicking and wind-sucking, and
78 locomotor behaviours, for instance pawing (Marsden, 2002; Cooper and
79 Albentosa, 2005). Prevalence estimates for these behaviours remain largely
80 unknown, and further investigation is warranted. Whether these abnormal
81 behaviours can strictly be classified as stereotypic according to the widely
82 accepted definition of stereotypy (above) is questionable, therefore this review will
83 focus primarily upon the three motor anomalies (crib-biting, weaving and box
84 walking) that reliably fit the commonly held definition.

85

86 Stereotypic behaviours are often viewed as 'vices' (McBride & Long, 2001), and
87 are associated with health complications. For example, crib-biting results in
88 excessive wear of the incisors, (McBride and Hemmings, 2009) and has been
89 proposed by some authors to increase the likelihood of colic (Archer et al., 1998),

90 although the underlying pathologic mechanisms are unknown. Weaving and box
91 walking have been associated with secondary muscle fatigue (Ninomiya et al.,
92 2007). Weaving is linked to weight loss (Mills and Davenport, 2002) and leg
93 swelling, and may ultimately result in lameness (Cooper et al., 2000). It is perhaps
94 because of these health impacts that there is a 37% reduction of monetary value
95 of stereotypy performing animals (Marsden, 2002; see also Williams and Randle –
96 this issue). Establishments including riding schools, racing and competition yards,
97 do not allow stereotypy performing animals onto the premises due to
98 unsubstantiated anecdotal belief that these behaviours are ‘copied’ from
99 stereotypy performing neighbours (Cooper and Albentosa, 2005). As such, 74%
100 riding schools, racing and competition yards investigated attempt to physically
101 prevent the behaviour (McBride and Long, 2001). Surgical procedures such as a
102 neurectomy or a myectomy, or the use of crib-straps or cribbing rings are
103 designed to prevent crib-biting behaviour (McBride and Long, 2001; McBride and
104 Hemmings, 2009; Albright et al., 2015). Despite their severity, these preventative
105 measures are not always effective (McBride and Hemmings, 2009), though in
106 some cases can result in a reduction in crib-biting behaviour (Albright et al., 2015).
107 Owners of weaving horses often utilise anti-weaving bars (McBride and Long,
108 2001), so the horse is unable to put the head outside of the stable to conduct the
109 behaviour (McAfee et al., 2002; McBride and Hemmings, 2009). This is often
110 unsuccessful as horses continue to weave within the confines of the stable
111 (McBride & Hemmings, 2009). Should the purpose of stereotypy be to provide a
112 coping mechanism for the individual, the physical prevention of these behaviours
113 could lead to further stress induced pathology (McGreevy and Nicol, 1998;
114 McAfee et al., 2002; Hemmings et al., 2004; Houpt, 2012; Freymond et al., 2015).
115 Indeed, following restriction of oral stereotypy with the use of a cribbing collar or
116 surgical methods, crib-biting horses were less able to cope during a stress test in
117 comparison to their counterparts who were not restricted from performing the crib-
118 biting response (Nagy et al., 2009). Underlying causal and contributory issues for
119 stereotypic behavior, e.g. poor environmental conditions, are seldom addressed,
120 and may not be known (Cooper and Mason, 1998; Cooper and Albentosa, 2005;
121 Nagy et al., 2009). We consider putative causal factors leading to stereotypy
122 manifestation and suggest separate developmental mechanisms for oral and
123 locomotory stereotypy of the horse.

124

125 Equine Oral Stereotypy: The Gastric Hypothesis

126 Gastric inflammation is common in crib-biting horses (Nicol et al., 2002; Cooper &
127 Albentosa, 2005), suggesting that gastrointestinal discomfort may be linked to the
128 development of this behaviour. Lending credence to this notion is the finding that
129 crib-biting is a predominantly post-prandial response (McBride & Hemmings,
130 2004). Horses evolved to consume a forage based diet, with approximately 16-
131 18h of the 24h time budget utilised for mastication in the wild (Cooper et al.,
132 2005), during which 35-40 litres of alkaline saliva is produced (Nicol et al., 2002;
133 Moeller et al., 2008; Nagy et al., 2010). Domesticated horses tend to be fed highly
134 palatable cereal based concentrate feeds to meet high energy requirements
135 (Hemmings et al., 2007; Albright et al., 2009; McBride and Hemmings, 2009;
136 Whisher et al., 2011) which reduces mastication, resulting in decreased saliva
137 production and increased acidity in the foregut (Nicol et al., 2002; Cooper and
138 Albentosa, 2005; Hemmings et al., 2007). This increased acidity may result in
139 gastric discomfort. Indeed, Nicol *et al* (2002) examined the equine gastric
140 environment endoscopically, comparing those which crib-bite and those who did
141 not exhibit oral stereotypy. Those who performed crib-biting demonstrated much
142 more stomach ulceration. Further study may wish to examine the gastric lining of
143 crib-biting animals and non-crib-biting animals kept under the same management
144 and feeding regimes, to truly dissect the gastric hypothesis of oral stereotypy.
145 Thus it has been hypothesized that the crib-biting response may attempt to
146 replicate the mastication process to stimulate salivary production (Nicol et al.,
147 2002; Hemmings et al., 2007; Moeller et al., 2008; Hothersall and Casey, 2012).
148 Saliva produced during crib-biting is similar in pH to saliva produced during
149 mastication (Moeller et al., 2008), which supports this idea. The function of crib-
150 biting could be to buffer the stomach in an attempt to counteract gastric pain
151 (Moeller et al., 2008) or acidosis of the hind-gut, and such a mechanism would be
152 consistent with the significant increase in crib-biting response 2-8 hours after
153 feeding (Clegg et al., 2008).

154

155 Evidence for this hypothesis includes that the addition of antacids to feed to
156 modulate gastric pH resulted in a significant reduction of observed crib-biting

157 (Mills and MacLeod, 2002; Nagy et al., 2010), and improved stomach lining
158 condition (Nicol et al., 2002). These positive results could also be attributed to
159 increased mastication of a feed, given a lower palatability following the addition of
160 powdered supplement.; this theory does require confirmation however. Resultant
161 increases in saliva would then lead to more effective gastric buffering (Johnson et
162 al., 1998). Cooper et al., (2005) found that increasing meal frequency also
163 resulted in a significant reduction in the crib-biting response, perhaps due to the
164 increased time taken to consume the ration, allowing a more effective buffering
165 effect of the saliva. *Ad lib* feeding studies have also produced mixed results (Fenn
166 et al., 2008; McCall et al., 2009) suggesting that the role of feeding regime in
167 stereotypy development requires further research.

168
169 Archer et al. (2008) provided support for the gut based hypothesis of crib-biting.
170 (Archer et al., 2008). Indeed, Archer *et al.* (2008) identified a strong, positive
171 association between presence of crib-biting and risk of developing colic. Whether
172 this relationship is causal or correlational is unknown (Cooper and Mason, 1998).
173 An episode of colic may result in chronic stress, an area of study that certainly
174 requires further investigation. Chronic stress in rodents contributes to
175 sensitisation of the dopaminergic midbrain and striatum in a genotype dependent
176 manner (Cabib et al., 1998) which has been hypothesized as a precursor for
177 stereotypy manifestation (McBride and Hemmings 2005). Colic could be an
178 initiating factor rather than an effect of crib-biting if the same processes occur in
179 horses.

180
181 To summarize, experimental evidence supports some link between feeding,
182 gastric discomfort and oral stereotypy, but it is currently difficult to conclude
183 whether stereotypy is an ameliorative response to stomach pathology, the
184 outcome of neural sensitisation induced by gastric stress, or an interaction
185 between these factors.

186 187 Equine Oral Stereotypy: The Dopaminergic Hypothesis

188 Chronic stress can have a significant influence on dopamine physiology,
189 particularly within the striatal brain regions (McBride and Hemmings, 2005).

190 Stressors commonly associated with stereotypy development such as feed
191 restriction and social isolation induce significant alterations to dopamine receptor
192 function in rodent models of spontaneous stereotypy (Cabib et al., 1998). Similar
193 changes were also observed in crib-biting horses by McBride and Hemmings
194 (2005) who found that D1 and D2 receptor densities were significantly increased
195 within the nucleus accumbens (NAcc), which is associated with sensitisation to
196 dopamine release within this ventral region. In contrast, D1 receptor density and D2
197 receptor affinity was reduced within the caudate nucleus, indicating reduced output
198 of this dorsal striatal structure in crib biting horses (McBride and Hemmings, 2005).
199 This study could not demonstrate whether these changes were present prior to the
200 emergence of crib-biting behaviour, or were as a result of crib-biting, but activity the
201 midbrain-striatum pathway is relevant for crib-biting horses. Changes within this
202 anatomical and neurochemical system may affect other aspects of the horse's
203 behavioural repertoire. The caudate nucleus is crucial to the process of action-
204 outcome monitoring. In rodent models of caudate inactivation, animals exhibit habit
205 formation (i.e., preferentially utilize a habitual response) far quicker than control
206 rodents (Yin et al., 2005). Similar acceleration in habit formation may be observed
207 in horses performing stereotypy. A cross maze test was examined striatal circuitry
208 within a sample of crib-biting versus control animals (Parker et al., 2009). Parker
209 and his co-workers observed that crib-biting animals demonstrated an accelerated
210 preference for a 'response' rather than a 'place' strategy, and as such were
211 preferentially utilising a habitual response rather than action-outcome monitoring.
212 This finding suggests that there is decreased output of the caudate nucleus,
213 resulting in an increased reliance on the sensorimotor putamen circuitry, resulting
214 in accelerated habit formation (Parker et al., 2008; 2009). Receptor based
215 alterations recorded by McBride and Hemmings (2005) may be probed using
216 carefully designed cognitive testing. Given the financial, logistical and ethical
217 dimensions of direct physiological measurements, cognitive tests have the potential
218 to significantly extend knowledge of stereotypy and associated neuro-mechanics.
219 Roberts et al. (2015) a proposed two basic inferred measures of dopamine
220 transmission consisting of spontaneous eye blink rate (SBR) and behavioural
221 initiation rate (BIR). Both were measured in triplicate over 30 minutes, SBR values
222 were obtained via counting of full blinks in the left eye at rest, where BIR records

223 the number of behavioural initiations i.e. the number of new behaviours performed,
224 also at rest.

225

226 Crib-biting horses demonstrated significantly decreased SBR, consistent with
227 studies that suggest lowered blink rate is indicative of dopamine receptor
228 sensitisation (Roebel and MacLean, 2007; Roberts et al., 2015). This result also
229 agrees with the receptor work conducted in the horse (McBride and Hemmings,
230 2005). The significantly increased BIR appears to indicate adaptations within the
231 dopamine circuitry of crib-biting animals, due to dominance of the movement
232 activating direct pathway over the movement inhibiting indirect pathway (Roberts
233 et al., 2015). Both the SBR and the BIR data appear to reflect the significant
234 adaptations of dopaminergic physiology previously recorded in crib-biting animals.
235 Further longitudinal study should reveal the scope of SBR and BIR and may
236 identify individuals predisposed to stereotypy development. If predictive potential
237 is revealed, given the pivotal role of chronic stress in stereotypy development, the
238 elimination of key stressors such as feed restriction and social isolation could
239 effectively reduce the risk that neural adaptations to receptor populations develop.
240 Insult to the gastric mucosa may also be associated with significant nociceptive
241 signalling to the CNS. Pain leads to liberation of neuropeptides such as beta
242 endorphin, which bind to mu receptor populations in the ventral tegmental area
243 (VTA), and contribute significantly to neuroplasticity in striatal brain regions (see
244 McBride and Hemmings 2009 for review). Therefore, a mechanism is proposed by
245 which a variety of environmental stressors lead to the neural changes that
246 underlie the emergence of stereotypy.

247

248 2.3 Equine Locomotor Stereotypy: Potential Aetiologies

249 Little work has been done on the specific aetiology of equine locomotor
250 stereotypy. McBride and Hemmings (2004) and Cooper and Albentosa (2005)
251 suggested that weaving is a pre-prandial response to highly palatable concentrate
252 feed, and others propose weaving occurs in response to high environmental
253 activity and anticipation (Cooper et al., 2000; Clegg et al., 2008).

254

255 Cooper et al. (2005) noted that the weaving response was significantly amplified
256 when concentrate meal frequency was increased. Interestingly, the control horses
257 whose meal frequency was not altered also performed an increase in locomotor
258 stereotypies when the experimental group were given their concentrate ration.
259 This may have been due to increased motivation to feed, suggesting that
260 locomotor stereotypy may well be an anticipatory response. This reasoning is
261 consistent with the pre-prandial nature of weaving behaviour (Cooper et al., 2005;
262 McBride and Parker, 2015).

263

264 Absence of social interaction has previously been associated with locomotor
265 stereotypic behaviour (Cooper et al., 2000; McAfee et al., 2002; Mills and
266 Reizebos, 2005), an important observation given that horses are by nature social
267 animals. When stable designs were adapted to allow the horses displaying a
268 stereotypy to observe other horses, the weaving response was significantly
269 reduced (Cooper et al., 2000). This result agrees with a recent study indicating that
270 adaptation of management regimes to include environmental enrichment such as
271 increasing contact with conspecifics resulted in a positive cognitive bias, i.e. an
272 improvement in affective state, in ambiguous situations (Löckener et al., 2016).
273 Simulation of social behaviours using a stable mirror was also associated with
274 reducing the weaving response (McAfee et al., 2002). It's unknown whether the
275 reduction was resultant from a perceived increase in social interaction or simply a
276 distracting stimuli, and as such requires further investigation (McAfee et al., 2002).
277 Mills and Reizebos (2005) attempted to resolve the relative potential roles of
278 social interaction versus distraction. When a poster with a two dimensional image
279 of a horse was present within the stable, the weaving response was significantly
280 reduced (Mills and Reizebos, 2005). This result may suggest that the reduction in
281 weaving response results from simulation of social behaviours. If so, weaving
282 may be linked to social contact, though the potential distracting effect of a novel
283 object may also have resulted in this reduction of weaving behaviour.

284

285 Weaving behaviour has also been attributed to lack of exercise (Cooper and
286 Mason, 1998). Weaving decreases with increased turnout and exercise (Cooper
287 et al., 2000). It is estimated that free-ranging horses take approximately 10,000
288 strides as part of their normal feeding regime within a social group per day. This
289 amount of exercise is a stark contrast to the confined stable situations under
290 which domesticated horses often live (Sarrafchi and Blokhuis, 2013). Increased
291 turnout also increases the opportunity for social interaction and improved grazing
292 activity. In this scenario social, exercise and nutritional requirements are met.
293 thereby the impetus for performing weaving behaviour is removed.

294

295 One recent study sought to investigate the potential neural mechanisms governing
296 weaving (Roberts et al., 2015). The SBR of the weaving animals was statistically
297 similar to the control group, but significantly increased when compared to the
298 crib-biting horses. SBR is believed to primarily controlled by midbrain projecting
299 areas originating in the substantia nigra, and terminating in the dorsal striatum
300 (see Karson 1983 for review). This finding suggests that dorsal striatal mechanics
301 are comparable to stereotypy-free control horses. Approach latency and task
302 acquisition were significantly faster in the weaving group. Heightened locomotion
303 (reflected in reduced approach latency) and faster task acquisition are largely
304 under ventral striatal control (see Robbins and Sahaikian, 1983 and Yin and
305 Knowlton, 2006 for respective reviews) suggesting elevated ventral activity and
306 normal functioning at the level of the dorsal striatum. This enhanced ventral
307 striatal functioning is further supported by a lack of habitual responding in weaving
308 animals, even after significant repetition of the operant response.

309

310 3.0 Motivational Basis of Stereotypic Behaviour

311 An understanding of motivational state during the development and ongoing
312 performance of stereotypy is important. Hughes and Duncan (1988) proposed a
313 generalised model (see Figure 1) to explain the motivational basis of a broad
314 range of behaviours whereby in response to organism variables (i.e., declining
315 blood glucose) the animal becomes motivated to perform a consummatory goal
316 (i.e., feeding) and thus appetitive strategies ensue. As an example, a horse may

317 have access to two fields, though preferentially graze in one field. When this field
318 has been grazed, the horse may experience reduced blood glucose levels. At this
319 point the consummatory goal is to graze. The appetitive behaviour is to get
320 additional food by moving from the first field to the adjoining field. The appetitive
321 phase has a positive feedback effect on motivation, and is therefore self-
322 reinforcing i.e., appetitive behaviours increase the motivation to continue to
323 perform appetitive behaviours until the consummatory goal has been met, in this
324 case ingesting grass from the neighbouring field. The achievement of the
325 consummatory goal has a number of effects: 1) functional consequence (e.g.,
326 elevated blood glucose), which leads to negative feedback on organism variables
327 with a subsequent effect on motivation; 2) direct feedback on motivation, initially
328 positive followed by negative; 3) an effect on perception of the animals
329 environment which again influences the underlying motivation of the behaviour.

330 **FIGURE 1 ABOUT HERE**

331

332 In the context of the Hughes and Duncan (1988) model, stereotypies have been
333 described as being appetitive in origin because the restrictive nature of the
334 animals' environment prevents the consummatory goal from being attained. Thus
335 a number of appetitive behaviours are being attempted in an effort to reach the
336 consummatory goal. Lack of consummation and subsequent functional
337 consequence means that no negative feedback on motivation to perform
338 appetitive behaviours occurs. Consequently, appetitive behaviours continue and
339 because they are self-reinforcing, the animal becomes locked in a positive feed-
340 back loop. The restrictive nature of the environment 'channels' the behaviour into
341 a limited number of discrete acts performed repeatedly. Over time, these
342 frustrated appetitive behaviours evolve into stereotypic motor sequences.

343

344 This model can now be updated to incorporate findings from recent studies
345 investigating locomotor versus oral stereotypy. Weaving seems to fit the Hughes
346 and Duncan model very well. Weaving animals are not pre-disposed to
347 accelerated habit formation, but do experience increased appetitive drive, perhaps
348 due to neural alterations that centre on ventral striatal circuitry (Roberts et al.,

349 2015). Weaving ensues whenever the consummatory goal (e.g., grazing, social
350 interaction) cannot be reached, though ceases when motivational end points (e.g.,
351 turnout, social interaction) are provided. Indeed, anecdotal observations appear to
352 support this notion, as weaving animals seldom perform stereotypy when turned
353 out to pasture.

354

355 Crib-biting persists despite achievement of the consummatory goal. The
356 recalcitrant nature of oral stereotypy reflects the tendency to rely on habitual
357 response patterns recorded in various investigations (Hemmings et al., 2007;
358 Parker et al., 2009). Indeed, minimal repetition of appetitive behaviour results in
359 transition to automatic habitual responding, divorced from conscious motivational
360 circuitry (see Figure 2).

361

362

363

364

FIGURE 2 ABOUT HERE

365 The ramifications of this extended model for management are twofold. First,
366 weaving can potentially be reduced by providing free access to consummatory
367 end points such as feeding and social interaction. Conversely, due the neural
368 differences that render crib-biting animals prone to habitual response patterns,
369 these animals will display considerable resistance to environmental intervention.
370 Thus, crib-biting behaviour will persist despite apparent consummatory end points
371 being reached. As such, a prophylactic approach to reducing occurrence of crib-
372 biting behaviour is recommended, perhaps with the use of predictive tools such as
373 SBR and BIR to identify predisposed animals and manage these animals
374 accordingly.

375

376

377 3.0 Conclusions

378 Crib-biting horses are initially in a high state of motivation, and as such attempt
379 appetitive behaviours (e.g., biting the stable door) in the face of poor
380 environmental conditions, particularly in relation to thwarted feeding behaviours
381 (e.g., lack of forage). Crib-biting is initially an appetitive behaviour and self-
382 reinforcing. Alterations within the ventral and dorsal striatum as a result of stress
383 and / or gastric pain increases the acceleration of habitual responding in crib-
384 biting animals. Thus the initial elevated motivation to perform crib-biting is
385 replaced with a habitual response pattern. As such, management regimes which
386 allow the consummatory goal to be achieved may not necessarily reduce crib-
387 biting behaviour. Neural changes may also account for the post-prandial increase
388 in the crib-biting response. Following ingestion of palatable feed, an opioid
389 mediated release of dopamine within the already sensitised striatum (McBride and
390 Hemmings, 2005; Whisher et al., 2011) correlates with a significantly increased
391 rate of the crib-biting response (Bachmann et al., 2003b; Whisher et al., 2011).

392

393 The weaving response appears to result from alterations to the ventral striatum
394 which lead to a highly motivated state, resulting in locomotor stereotypy due to an
395 unattainable consummatory goal. Weaving animals do not exhibit an accelerated
396 reliance on habitual response mechanisms, and as such management strategies
397 (e.g., increasing turnout) to reduce performance of locomotor stereotypy is worth
398 attempting, by ensuring that the horse's innate needs are met.

399

400 Finally, both oral and locomotor stereotypies of the horse appear to involve
401 neuroplasticity at the level of the striatal group of brain structures. In rodent
402 species the function of these varies with genetic strain. The identification of
403 genetic polymorphisms that may place horses at increased risk of stereotypy
404 development deserve more research. The technology now exists to enable in-
405 depth genetic research strategies. Following identification of predisposed animals,
406 removal of key stressors will provide immense potential for prevention over and
407 above unpredictable remedial measures.

408

409 **Conflict of interest statement:** There are no conflicts of interest relevant to this
410 manuscript

411

412 **Ethical Approval:** Not required

413 This invited review was written with an equal contribution of all stated authors.

414

415 **Reference List**

416

417 Albright JD, Mohammed HO, Heleski CR, Wickens CL, Houpt KA., 2009. Crib-
418 biting in US horses: breed predispositions and owner perceptions of aetiology.
419 Equine. Vet. J. 5, 455-8.

420

421 Albright, J. D., Witte, T. H., Rohrbach, B. W., Reed, A., Houpt, K. A., 2015.
422 Efficacy and effects of various anti-crib devices on behaviour and physiology of
423 crib-biting horses. Equine Vet. J. 48(6), 727-731.

424

425 Archer, D. C., Pinchbeck, G. L., French, N. P., Proudman, C. J., 2008. Risk
426 factors for epiploic foramen entrapment colic: an international study. Equine Vet.
427 J. 40(3), 224-230.

428

429 Bachmann, I., Audigé, L., Stauffacher, M., 2003a. Risk factors associated with
430 behavioural disorders of crib-biting, weaving and box-walking in Swiss horses.
431 Equine Vet. J. 35(2), 158-163.

432

433 Bachmann, I., Bernasconi, P., Herrmann, R., Weishaupt, M. A., Stauffacher, M.,
434 2003b. Behavioural and physiological responses to an acute stressor in crib-biting
435 and control horses. Appl. Anim. Behav. Sci. 82(4), 297-311.

436

437 Cabib, S., Giardino, L., Calza, L., Zanni, M., Mele, A., Puglisi-Allegra, S., 1998.
438 Stress promotes major changes in dopamine receptor densities within the
439 mesoaccumbens and nigrostriatal systems. Neuroscience. 84, 193-200.

440

441 Cabib, S., 2006. The Neurobiology of Stereotypy II: The Role of Stress. In: Mason,
442 G. & Rushen, J. eds. Stereotypic Animal Behaviour Fundamentals and
443 Applications to Welfare. 2nd ed. CABI International, Oxfordshire, pp. 227-255.

444

445 Clegg, H.A., Buckley, P., Friend, M.G., McGreevy, P.D., 2008. The ethological
446 and physiological characteristics of cribbing and weaving horses. *Appl. Anim.*
447 *Behav. Sci.* 109, 68-76.

448

449 Cooper, J.J., Albentosa, M.J., 2005. Behavioural adaptation in the domestic
450 horse: potential role of apparently abnormal responses including stereotypic
451 behaviour. *Livest. Prod. Sci.* 92(2), 177-182.

452

453 Cooper, J.J., Mason, G.J., 1998. The identification of abnormal behaviour and
454 behavioural problems in stabled horses and their relationship to horse welfare: a
455 comparative review. *Equine Vet. J.* 30(S27), 5-9.

456

457 Cooper, J.J., McCall, N., Johnson, S., Davidson, H.P.B., 2005. The short-term
458 effects of increasing meal frequency on stereotypic behaviour of stabled horses.
459 *Appl. Anim. Behav. Sci.* 90(3-4), 351-364.

460

461 Cooper, J.J., McDonald, L., Mills, D.S., 2000. The effect of increasing visual
462 horizons on stereotypic weaving: Implications for the social housing of stabled
463 horses. *Appl. Anim. Behav. Sci.* 69, 67-83.

464

465 Fenn, T.R., McCall, C.A., Eckert, C.E., Brown, W.H., McElhenney, W.H., 2008.
466 Effect of ad libitum concentrate feeding on cribbing behaviour in horses. *J. Anim.*
467 *Sci.* 86(S2), 516.

468

469 Freymond, S.B., Bardou, D., Briefer, E.F., Bruckmaier, R., Fouché, N., Fleury, J.,
470 Maigrot, A.L., Ramseyer, A., Zuberbühler, K., Bachmann, I., 2015. The
471 physiological consequences of crib-biting in horses in response to an ACTH
472 challenge test. *Physiol. Behav.* 151, 121-128.

473

474 Hemmings, A., McBride, S.D., Hale, C.E., 2007. Perseverative responding and the
475 aetiology of equine oral stereotypy. *Appl. Anim. Behav. Sci.* 104 (1-2), 143-150.

476

477 Hemmings, A.J., McBride, S.D., Smith, N.C., 2004. The putative reward function
478 of equine stereotypic behaviour. In: Alliston, J., Chadd, S., Ede, A., Longland, A.,
479 Moore-Colyer, M., Hemmings, A., Hyslop, J. eds. *Emerging Equine Science*.
480 Nottingham University Press Nottingham, pp. 67-79.

481

482 Henderson, A.J.Z., 2007. Don't fence me in: Managing psychological well being
483 for elite performance horses. *J. Appl. Anim. Welf. Sci.* 10(4), 309-329.

484

485 Hillyer, M. H., Taylor, F. G. R., Proudman, C. J., Edwards, G. B., Smith, J. E.,
486 French, N. P., 2002. Case control study to identify risk factors for simple colonic
487 obstruction and distension colic in horses. *Equine Vet. J.* 34(5), 455-463.

488

489 Hothersall, B., Casey, R., 2012. Undesired behaviour in horses: A review of their
490 development, prevention, management and association with welfare. *Equine Vet.*
491 *Educ.* 24(9), 479-485.

492

493 Houpt, K.A., 2012. Motivation for cribbing by horses. *Anim. Welfare.* 21, 1-7.

494

495 Hughes, B. O., Duncan, I. J. H., 1988. The notion of ethological need, models of
496 motivation and animal welfare. *Anim Behav.* 36, 1696-1707

497

498 Ikemoto, S., Panksepp, J., 1996. Dissociations between appetitive and
499 consummatory responses by pharmacological manipulations of reward-relevant
500 brain regions. *Behav. Neurosci.* 110, 331-345

501

502 Johnson, K.G., Tyrrell, J., Rowe, J.B., Pethick, D.W., 1998. Behavioural changes
503 in stable horses given nontherapeutic levels of virginiamycin. *Equine Vet. J.* 30,
504 139-143.

505

506 Löckener, S., Reese, S., Erhard, M., Wöhr, A. C., 2016. Pasturing in herds after
507 housing in horseboxes induces a positive cognitive bias in horses. *J. Vet. Behav.*
508 11, 50-55.

509

510 Malamed, R., Berger, J., Bain, M. J., Kass, P., Spier, S. J., 2010. Retrospective
511 evaluation of crib-biting and windsucking behaviours and owner-perceived
512 behavioural traits as risk factors for colic in horses. *Equine Vet. J.* 42(8), 686-692.

513

514 Malmkvist, J., Poulsen, J. M., Luthersson, N., Palme, R., Christensen, J. W.,
515 Søndergaard, E., 2012. Behaviour and stress responses in horses with gastric
516 ulceration. *Appl. Anim. Behav. Sci.* 142(3), 160-167.

517

518 Mason, G., 2006. The Neurobiology of Stereotypy II: The Role of Stress. In:
519 Mason, G. & Rushen, J. eds. *Stereotypic Animal Behaviour Fundamentals and*
520 *Applications to Welfare*. 2nd ed. CABI International, Oxfordshire, pp. 325-356.

521

522 Marsden, D., 2002. A new perspective on stereotypic behaviour problems in
523 horses. *In Practice*. 24(10), 558-569.

524

525 McAfee, L.M., Mills, D.S., Cooper, J.J., 2002. The use of mirrors for the control of
526 stereotypic weaving behaviour in the stabled horse. *Appl. Anim. Behav. Sci.* 78(2),
527 159-173.

528

529 McBride, S.D., Hemmings, A., 2004. Causal factors of equine stereotypy. In:
530 Alliston, J., Chadd, S., Ede, A., Longland, A., Moore-Colyer, M., Hemmings, A.,
531 Hyslop, J. eds. *Emerging Equine Science*. Nottingham University Press
532 Nottingham, pp 35-65.

533

534 McBride, S.D., Hemmings, A.J., 2005. Altered mesoaccumbens and nigro-striatal
535 dopamine physiology is associated with stereotypy development in a non-rodent
536 species. *Behav. Brain Res.* 159, 113-118.

537

538 McBride, S.D., Hemmings, A.J., 2009. A neurologic perspective of equine
539 stereotypy. *J. Equine Vet. Sci.* 29, 10-16.

540

541 McBride, S.D., Long, L., 2001. The perception and subsequent management of
542 equine stereotypic behaviour by horse owners; implications for animal welfare.
543 *Vet. Rec.* 148, 799-802.

544

545 McBride, S. D., Parker, M. O., 2015. The disrupted basal ganglia and behavioural
546 control: An integrative cross-domain perspective of spontaneous stereotypy.
547 *Behav. Brain Res.* 276, 45-58.

548

549 McCall, C.A., Tyler, P.J., McElhenney, W.H., Fenn, T.R., 2009. Effect of hourly
550 concentrate feed delivery on crib-biting in Thoroughbred horses. *J. Equine Vet.*
551 *Sci.* 29(5), 427-428.

552

553 McGreevy, P.D., Nicol, C.J., 1998. The effect of short term prevention on the
554 subsequent rate of crib-biting in Thoroughbred horses. *Equine Vet. J. Suppl.*
555 30(27), 30-34.

556

557 McGreevy, P.D., French, N.P., Nicol, C.J., 1995. The prevalence of abnormal
558 behaviours in dressage, eventing and endurance horses in relation to stabling.
559 Vet. Rec. 137, 36-37.

560

561 Mills, D., Davenport, K., 2002. The effect of a neighbouring conspecific versus the
562 use of a mirror for the control of stereotypic weaving behaviour in the stabled
563 horse. Anim. Sci. 74(1), 95-101.

564

565 Mills, D.S., MacLeod, C.A., 2002. The response of crib-biting and windsucking in
566 horses to dietary supplementation with an antacid mixture. Ippologia 13, 33–41.

567

568 Mills, D.S., Riezebos, M., 2005. The role of the image of a conspecific in the
569 regulation of stereotypic head movements in the horse. Appl. Anim. Behav. Sci.
570 91, 155-165.

571

572 Mills, D.S., Alston, R.D., Rogers, V., Longford, N.T., 2002. Factors associated with
573 the prevalence of stereotypic behaviour amongst Thoroughbred horses passing
574 through auctioneer sales. Appl. Anim. Behav. Sci. 78(2-4), 115-124.

575

576 Moeller, B.A., McCall, C.A., Silverman, S.J., McElhenney, W.H., 2008. Estimation
577 of saliva production in crib-biting and normal horses. J. Equine Vet. Sci. 28(2), 85-
578 90.

579

580 Nagy, K., Bodó, G., Bárdos, G., Harnos, A., Kabai, P., 2009. The effect of a
581 feeding stress-test on the behaviour and heart rate variability of control and crib-
582 biting horses (with or without inhibition). Appl. Anim. Behav. Sci. 121(2), 140-147.

583

584 Nagy, K., Bodó, G., Bárdos, G., Bánszky, N., Kabai, P., 2010. Differences in
585 temperament traits between crib-biting and control horses. *Appl. Anim. Behav.*
586 *Sci.* 122(1), 41-47.

587

588 Nicol, C.J., Davidson, H.P.D., Harris, P.A., Waters, A.J., Wilson, A.D., 2002. Study
589 of crib-biting and gastric inflammation and ulceration in young horses. *Vet. Rec.*
590 151(22), 658-662.

591

592 Ninomiya, S., Sato, S., Sugawara, K., 2007. Weaving in stabled horses and its
593 relationship to other behavioural traits. *Appl. Anim. Behav. Sci.* 106(1-3), 134-143.

594

595 Parker, M., McBride, S.D., Redhead, E.S., Goodwin, D., 2009. Differential place
596 and response learning in horses displaying an oral stereotypy. *Behav. Brain Res.*
597 200, 100-105.

598

599 Parker, M., Redhead, E.S., Goodwin, D., McBride, S.D., 2008. Impaired
600 instrumental choice in crib-biting horses (*Equus caballus*). *Behav. Brain Res.* 191,
601 137-140.

602

603 Pell, S.M., McGreevy, P.D., 1999. A study of cortisol and beta-endorphin levels in
604 stereotypic and normal Thoroughbreds. *Appl. Anim. Behav. Sci.* 64(2), 81-90.

605

606 Roberts, K., Hemmings, A.J., Moore-Colyer, M., Hale, C., 2015. Cognitive
607 differences in horses performing locomotor versus oral stereotypic behaviour.
608 *Appl. Anim. Behav. Sci.* 168, 37-44.

609

610 Robbins, T.W., Sahaikian, B.J., 1983. Behavioral effects of psychomotor stimulant
611 drugs: clinical and neuropsychological implications, In: Creese, I. (Ed.) *Stimulants,*
612 *neurochemical, behavioral, and clinical perspectives,* Raven Press.

613

614 Roebel, A.M., & MacLean, W.E., 2007. Spontaneous eye-blinking and stereotyped
615 behaviour in older persons with mental retardation. *Res. Dev. Disabil.* 28, 37-42.

616

617 Sarrafchi, A., Blokhuis, H. J., 2013. Equine stereotypic behaviors: causation,
618 occurrence, and prevention. *J. Vet. Behav.* 8(5), 386-394.

619

620 Whisher, L., Raum, M., Pina, L., Pérez, L., Erb, H., Houpt, C., Houpt, K., 2011.
621 Effects of environmental factors on cribbing activity by horses. *Appl. Anim. Behav.*
622 *Sci.* 135(1), 63-69.

623

624 Wickens, C.L., Heleski, C.R., 2010. Crib-biting behaviour in horses: a review.
625 *Appl. Anim. Behav. Sci.* 128(1-4), 1-9.

626

627 Williams and Randle.

628

629 Yin, H. H., Ostlund, S. B., Knowlton, B. J., Balleine, B. W., 2005. The role of the
630 dorsomedial striatum in instrumental conditioning. *Eur. J. Neurosci.* 22, 513-23.

631

632 Yin, H.H., Knowlton, B.J., 2006. The role of the basal ganglia in habit formation.
633 *Nature Rev. Neurosci.* 7, 464-476.