2017-09-23

Abnormal repetitive behaviours in captive birds: a Tinbergian review

Mellor, E

http://hdl.handle.net/10026.1/10137

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Keywords: bird welfare; abnormal repetitive behaviour; causation; development; evolution;

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function.

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Abstract

Abnormal repetitive behaviours (ARBs) are associated with past, or present, welfare

problems and are common elements of the behavioural repertoire of some captive animals,

including birds. Millions of birds from thousands of species are held in various captive

settings, yet most avian ARB research to-date focuses on just a handful of these. Therefore,

our knowledge of ARBs and, by implication, welfare, of a taxonomically diverse range of

avian species is poorly understood. The purpose of this review is to begin to address this by

providing a useful overview of ARBs across captive avian species. Taking advantage of the

research effort on well-studied species, we pool current findings relating to avian ARBs into

a coherent framework, highlight gaps in understanding, and use this to give a reference point

for future research in both these and other species. We adopt Tinbergen's 'Four Questions'

approach to comprehensively consider ARBs from each of his four perspectives. We begin

with presenting studies on ARB development, describe how physiological predispositions

and early-life housing and experiences impact ARB risk in later life. Next we outline internal

causal triggers for ARBs, such as the effects of neurotransmitters, hormones, and dietary

deficiencies, and discuss external, environmental triggers for ARBs. In the evolution section,

we detail the influence of species' evolutionary history on ARB, and use findings from early

molecular studies on laying hens to discuss heritability and genes associated with ARB. The

benefits of using cross-species studies to determine underlying evolutionary drivers of ARBs

are also illustrated with an example from Psittaciformes. In discussing ARB 'function', we

make two tentative suggestions for potential examples of ARB performance allowing a bird

to cope, and also consider situations where ARB may be functionless. We then summarise,

and discuss, these four interacting perspectives on avian ARBs. To finish, the benefits of

Tinbergen's approach are shown in a worked example of an ARB in one species,

demonstrating how this valuable framework leads to the most complete understanding of

ARB. Thus, by utilising Tinbergen's Four Questions, our review provides a platform for future

42   research on avian ARBs, to lead to a better understanding of ARBs in both well- and poorly-

43   studied species, and to solutions/preventive measures to improve avian welfare.

44

1. Introduction

Abnormal repetitive behaviours (ARBs) are a common element of the behavioural repertoire of some captive animals (Mason, 1991b; Garner and Mason, 2002). Here, we use 'ARB' to encompass highly repetitive and invariant 'stereotypies' (Ödberg, 1978; Mason, 1991b) and more variable compulsive/impulsive behaviours like feather-pecking/plucking (reviewed by: Garner, 2006). ARBs are associated with past or present welfare problems (Mason, 2006b), such as the experience of impoverished environments (Hediger, 1950; Morris, 1964; Carlstead, 1998), or when highly motivated behaviours cannot be performed (*e.g.* in mice, *Mus musculus*: Würbel, Stauffacher & von Holst, 1996). Performance of ARB can both reflect and exacerbate poor welfare situations; for example, pacing in captive Carnivora sometimes causes abrasions, sores and abscesses (Morris, 1964; Meyer-Holzapfel, 1968; Mason, 1991a). ARBs also cause problems for animal-human interactions: ARB-performance is generally negatively perceived (*e.g.* in zoo animals: Miller, 2012), reduces the desirability of companion animals (ARB can result in pet relinquishment: Marston et al., 2004; Gaskins, 2011), and can reduce the monetary value of animals *(e.g.* horses*, Equus caballus*, with ARB: McBride and Long, 2001).

ARBs in mammals have been well documented and reviewed (*e.g.* Bashaw, Tarou, Maki & Maple, 2001; Benhajali, Exxaouia, Lunel, Charfi, & Hausberger, 2014; Clubb & Mason 2007; Mason, 1991; Sahakian, Robbins, Morgan, & Iverson, 1975), but the same is not true for most avian species (but see: van Hoek and Ten Cate, 1998). Millions of captive birds from thousands of species are housed in zoos (Conde et al., 2011), used for research purposes (annually, approximately 151,000 - 215,000 passerines: Bateson and Feenders, 2010), farmed for food (worldwide, an estimated 9.5 billion laying hens, *Gallus gallus domesticus,* and 71 billion broilers were produced in 2014: FAO, 2014), and as pets (*e.g.* in North America there are around 10 million pet parrots: Tweti, 2008). Despite this, the vast majority

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70   of published literature is biased towards two species, domestic chickens, and European

71   starlings, *Sturnus vulgaris*, and one order: Psittaciformes (parrots). Knowledge surrounding

72   avian ARBs and, implicitly, welfare across this taxonomically diverse range of species

73   remains currently limited to issues specific to these species. To address these issues, a

74   holistic consideration of avian ARBs, permitting clear, broad predictions about susceptibility,

75   amelioration and impact, across species and situations is now required.

76   The purpose of this review, therefore, is to provide a useful overview of ARBs across captive

77   birds, taking advantage of the research effort on well-studied species, to give a starting point

78   for future research. Tinbergen (1963) advocated that a comprehensive understanding of

79   behaviour is only possible via a framework of posing 'Four Questions' (see also: Bateson

80   and Laland, 2013). Thus, this review will follow his framework. Firstly, we address the

81   proximate questions: development (how has the individual's ARB developed over time?),

82   and causation (what are the internal and/or external mechanisms that trigger ARB?) (Mayr,

83   1961; Klopfer and Hailman, 1972). Next, we consider the ultimate questions: evolution (how

84   can evolutionary history and genetics shape ARB?), and function (what is the value, if any,

85   of ARB to the individual?) (Mayr, 1961; Klopfer and Hailman, 1972).

86   ## 2. ARBs in birds

87   Table 1 summarises avian ARBs reported in the literature, loosely grouped based on

88   similarities in outward form. Whether the superficial resemblance of some ARBs across

89   different species is underpinned by shared causality is an important question that should be

90   addressed in the future. Presently, however, there is not sufficient information to take an

91   informed approach, an issue which further emphasises the need for this review. Therefore,

92   our groupings are based on physical similarity and, importantly, do not imply similarity of

93   development, causation, evolution or function (though we do not discount that future work

94   might demonstrate such homologies).

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Table 1. Table summarising ARBs performed by various species of captive bird. Note that we have loosely grouped ARBs by the outward physical appearance of the ARB itself for convenience only. Our schema should not be taken to imply between-species similarity in causation, development, evolution or function: we encourage others to refute or provide future evidence for the existence of such similarities. Additionally, we anticipate that ARB is not restricted to these species and forms we give here, but until such reports are published we are limited to the examples we provide below.

Specific definitions or descriptions of ARB	Affected species reported
Feather-directed ARBs	
FDB: bird repetitively chews, bites, and/or plucks out its feathers, usually self-directed, but occasionally aimed at cage-mates (van Zeeland et al., 2009)	Psittaciformes (Meehan et al., 2003; van Zeeland et al., 2009; McDonald Kinkaid, 2015)
Feather-pecking: can be divided into two subtypes. *Gentle feather pecks*: nibbling and pecking without removal of the feather (Dixon et al., 2008; Dalton et al., 2013), suggested to relate to normal exploratory pecking of conspecifics (Riedstra and Groothuis, 2002). Can be 'stereotyped' in form when performed a rapid rate repeatedly at one location of the recipient (Newberry et al., 2007; Rodenburg et	Domestic chickens, *Gallus gallus domesticus,* layers and broiler breeders (Savory, 1995; De Jong and Guémené, 2011) Red jungle fowl, *Gallus gallus* (Jensen et al., 2005) Pheasants, *Phasianus colchicus* (Butler and Davis, 2010) Turkeys, *Meleagris gallopavo* (Dalton et al., 2013) Domestic ducks, *Anas platyrhynchos domesticus* (Rodenburg et al.,

al., 2013). *Severe feather pecks*: painful pulling or removal of the feather (McAdie and Keeling, 2002; Newberry et al., 2007; Dixon et al., 2008; Rodenburg et al., 2013). Clearly feather-pecking, notably the severe form, compromises the welfare of the recipient, but it also indicates that the welfare of the performer has been compromised, either currently and/or previously (*e.g.* Bolhuis et al., 2009; Brunberg et al., 2016).

2005; Gustafson et al., 2007)

Muscovy ducks, *Cairina moschata* (Rodenburg et al., 2005; Gustafson et al., 2007)

'Excessive' feather-plucking (Harvey et al., 2002)

Hawaiian crows, *Corvus hawaiiensis* (Harvey et al., 2002)

Feather-picking: bird aggressively pecks at the feathers from the back and tail areas of pen-mates (Samson, 1996)

Ostriches, *Struthio camelus* (Samson, 1996)

Locomotor ARBs: repetitive patterns of identical locomotion

Route-tracing: repetitive tracing of a route within the cage. May include the perch, floor, cage walls, as well as airborne elements (Keiper, 1969; Garner et al., 2003; Meehan et al., 2004; Feenders and Bateson, 2012)

Psittaciformes (Meehan et al., 2004; McDonald Kinkaid, 2015)

Laying hens (Duncan and Wood-Gush, 1972)

Blue tits, *Cyanistes caeruleus* (Garner et al., 2003)

Marsh tits, *Poecile palustris* (Garner et al., 2003)

	European starlings, *Sturnus vulgaris* (Feenders and Bateson, 2012)
and/or	Canaries, *Serinus canaria domestica* (Keiper, 1969)
	Green singing finches, *Serinus mozambicus* (Keiper, 1969)
Pacing: moving forwards and back linearly along the ground, usually	Gray singing finches, *Serinus leucopygius* (Keiper, 1969)
next to a cage wall or fence (Duncan and Wood-Gush, 1972; Degen	Blue jays, *Cynanocitta cristata* (Keiper, 1969)
et al., 1989; Glatz, 2000; Meehan et al., 2004)	Slate coloured juncos, *Junco hyemalis* (Keiper, 1969)
	Tree sparrows, *Spizella arborea* (Keiper, 1969)
	Zebra finches, *Taeniopygia guttata* (Jacobs et al., 1995)
	Emus, *Dromaius novaehollandiae* (Glatz, 2000)
	Ostriches (Degen et al., 1989)
	Japanese quails, *Coturnix japonica* (Saint-Dizier et al., 2008; Laurence et al., 2015)
Somersaulting: repeated completion of a backward aerial flip, with the legs passing above the bird's head (Feenders and Bateson, 2012) *	European starlings (Feenders and Bateson, 2012)

Other locomotor ARBs: repetitive patterns of identical partial or whole-body locomotor movements

Spinning, rocking, twirling movements of the body or head (Meehan	Psittaciformes (Meehan et al., 2004; McDonald Kinkaid, 2015)

et al., 2004; McDonald Kinkaid, 2015)

Behavioural star-gazing: bird continually lifts the head up and back towards the spine (seemingly unrelated to a similar action induced by thiamine deficiency in poultry) (Samson, 1996)	Ostriches (Samson, 1996)

Oral ARBs: repetitive patterns of identical oral movements

Wire-chewing, sham-chewing, food manipulation, dribbling (Meehan et al., 2004; McDonald Kinkaid, 2015; Polverino et al., 2015)	Psittaciformes (Meehan et al., 2004; McDonald Kinkaid, 2015; Polverino et al., 2015)
Spot-picking/pecking: bird repeatedly touches the tip or the side of its beak, or pecks, either itself or objects such as empty feeders, walls and drinkers (Keiper, 1969; D'Eath et al., 2009)	Broiler breeders (D'Eath et al., 2009) Canaries (Keiper, 1969) Green singing finches (Keiper, 1969) Gray singing finches (Keiper, 1969) Blue jays (Keiper, 1969) Japanese quails (Castagna et al., 1997)

*The following ARBs appear to be functionally related to somersaulting in European starlings. *Head tilt*: the bird tilts its head back and the beak breaks the vertical plane (Brilot et al., 2009). *Loop*: very similar to a somersault, but the bird briefly clings to the cage ceiling, wall or perch with its feet. *Fall*: bird 'falls' backwards off its perch. *Back-flip*: movement on the floor resembling a somersault but minus the loop component (Feenders and Bateson, 2012).

95 Regarding feather-pecking (FP) in chickens, there are two forms commonly reported in the

96 literature: severe and gentle (see Table 1). Herein, we indicate specific form if it has been

97 reported, though this has not been always possible as authors do not always discriminate

98 between the two (practically, this can be difficult for large flocks of birds). As will be seen, the

99 two forms of FP have different welfare implications (*e.g.* McAdie and Keeling, 2000), and

100 cases in which the two are pooled complicates the understanding of the basis for each. For

101 this reason, we strongly encourage researchers during future studies to discriminate

102 between the two forms of FP wherever possible.

103 ***TABLE 1 ABOUT HERE, PLEASE***

2.1 Development

105 Development examines behavioural development over an individual's lifetime. Past

106 experiences, life-stage (*i.e.* chick, juvenile, and adult), and hormonal and physiological

107 profile all shape behaviour and susceptibility to ARB development.

2.1.1 Developmental trajectory of ARB

109 Several longitudinal studies have demonstrated the developmental trajectory of FP in laying

110 hens (Huber-Eicher and Sebö, 2001; Lambton et al., 2010; Gilani et al., 2013). There is

111 generally good agreement across studies that the prevalence and rates of the more

112 damaging, severe FP increases as hens age, *e.g.* from 27% and 0.4 bouts per bird per hour

113 during rear, to 65% and 1.9 bouts per bird per hour during lay (Gilani et al., 2013). The

114 developmental trajectory of gentle FP is different, however, and either does not change or

115 declines (*e.g.* Lambton et al., 2010; Gilani et al., 2013); supporting the argument that gentle

116 and severe FP are different behaviours, with different welfare outcomes.

117 Although FP development is perhaps the best studied avian ARB, two longitudinal studies on

118 orange-winged Amazon parrots, *Amazona amazonica* examined the development of several

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119 ARBs in this species (Meehan et al., 2004). Two groups of birds, raised identically (captive-

120 bred and parent-reared), were observed for 48 weeks from the age of 18-weeks. Whilst all

121 were housed individually, 'enriched' parrots received foraging and physical enrichments,

122 whereas 'control' parrots did not (Meehan et al., 2004). Control parrots developed oral and

123 locomotor ARBs significantly sooner and more severely than enriched parrots, especially

124 during the first 16 weeks (Meehan et al., 2004). While it is expected that ARBs increase

125 during development if conditions remain unchanged, improving the environment, as

126 demonstrated in this study, can slow their development. Hence, control parrots' ARBs were

127 significantly reduced when the enrichments were later provided (Meehan et al., 2004). Using

128 the same experimental set up as above, this research group also reported a similar

129 reduction in feather-damaging behaviour (FDB, see Table 1 for a description), again though

130 enrichment provision (Meehan et al., 2003b).

131 *2.1.2 Physiological development and ARBs*

132 *2.1.2.1 Sex*

133 In some species, female birds are at increased risk of feather-directed behaviours, such as

134 FP and FDB (Jensen et al., 2005; Garner et al., 2006; Mellor, 2014). For instance, 18% of

135 females *versus* 7.9% of males feather-pecked in a red-jungle fowl, *Gallus gallus*, X white

136 leghorn (a laying strain) population (Jensen et al., 2005), and female parrots are more FDB

137 prone (McDonald Kinkaid et al., 2013; Mellor, 2014). Causal factors behind this female-bias

138 are detailed in Section 2.2.1.3, but briefly the onset of lay (and associated rises in

139 progesterone and oestrogen) is a key time in FP development (Hughes, 1973). The same is

140 suggested to be true in FDB (Wedel, 1999), though experimental evidence for this is

141 currently lacking.

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142   *2.1.2.2 Personality and stress response style*

143   Personality, defined as consistent behavioural differences between individuals of the same

144   species (Nettle and Penke, 2010), also relates to ARB. Orange-winged Amazon parrots with

145   FDB showed more neuroticism-type personality traits, such as 'fearfulness' and 'excitability',

146   whereas extraversion-type traits were negatively associated with locomotor ARBs (Cussen

147   and Mench, 2015). The authors suggested personality influences an individual's

148   susceptibility to environmental stressors, here during enrichment deprivation, and thus ARB

149   (Cussen and Mench, 2015).

150   Stress response style, or 'coping' style, a set of consistent behavioural and physiological

151   responses to stress (Koolhaas et al., 1999), also affects susceptibility to ARB development.

152   Two response styles are recognised, each with distinctive behaviours and physiological

153   characteristics. 'Proactive' individuals have an active behavioural stress response, are 'bold'

154   (*e.g.* will approach unfamiliar objects, *sensu*: Wilson et al., 1994), aggressive, impulsive, and

155   are inclined towards routine formation (Koolhaas et al., 1999). 'Reactive' individuals have a

156   passive behavioural stress response, are 'shy' (*e.g.* unlikely to approach unfamiliar objects,

157   *sensu*: Wilson et al., 1994), are less aggressive, avoid risks, and behave flexibly (Koolhaas

158   et al., 1999). Proactive individuals are characterised by low hypothalamus-pituitary-adrenal

159   axis responsiveness and high sympathetic reactivity, whereas the opposite occurs in

160   reactive individuals (Koolhaas et al., 1999). These differences in response style are

161   suggested to predispose proactive individuals to ARB development (Koolhaas et al., 1999;

162   Ijichi et al., 2013) with neurobiological differences being particularly influential (detailed in

163   Section 2.2.1.2).

164   There are two avian examples of proactive susceptibility to ARB. Two strains of white

165   leghorn chicken with contrasting propensity to FP also show differential response styles:

166   high FPs tend to be proactive, and low FPs reactive (Blokhuis and Beutler, 1992; van

167   Hierden et al., 2002a; van Hierden et al., 2002b). In African grey parrots, *Psittacus erithacus*,

168 van Zeeland et al. (2013b) found some indication that parrots with FDB may have a

169 proactive response style, but this was not consistent across different experiments. FDB

170 status did not predict response style during a stressful event (manual restraint), but during

171 novel object and open field tests parrots with FDB adopted a proactive style (van Zeeland et

172 al., 2013b), *i.e.* they were bolder, and more likely to approach a novel object and explore

173 during an open field test than birds without FDB.

174 *2.1.3 Past experiences and ARBs*

175 *2.1.3.1 Rearing conditions*

176 Rearing conditions experienced during early life influence ARB development. In laying hens,

177 brooded (hen-reared) chicks are at less risk of developing FP when older (Perré et al., 2002)

178 and are less likely to suffer FP and cannibalism-related mortality (Riber et al., 2007). Hand-

179 reared African grey parrots (from 5 weeks old or less) are at increased risk of ARB as adults

180 and are also more aggressive towards humans (Schmid et al., 2006). Contrastingly, though

181 not directly comparable as all parent-reared birds were also wild-caught, hand-reared

182 European starlings are less likely to perform somersaulting and other ARBs (Feenders and

183 Bateson, 2012; but see: Coulon et al., 2014), are less fearful of humans (Feenders and

184 Bateson, 2011), and do not show any indications of compromised cognitive function

185 (Feenders and Bateson, 2013). As European starlings do not readily breed in captivity

186 (Bateson and Feenders, 2010), whether this effect is one of hand-rearing or origin (wild

187 *versus* captive) is unknown.

188 While not totally clear-cut in some cases, wild-caught birds may be more likely to develop

189 ARBs than captive-bred. Wild-caught African grey parrots are more likely to display FDB

190 than captive-bred individuals, regardless of captive-rearing technique (Schmid et al., 2006).

191 Similarly, Keiper (1969) found his wild-caught blue jays, *Cyanocitta cristata*, performed more

192 route-tracing but less spot-picking than captive-raised counterparts. This blue jay example

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193   suffers from the same confound as with the starlings, as captive-raised birds were all hand-

194   reared, leaving it impossible to judge the most influential developmental factor.

195   Aside from parental contact, other appropriate conspecific social experiences can be

196   important to young birds. Solitary- and hand-reared captive Hawaiian crows, *Corvus*

197   *hawaiiensis,* show more ARB as adults compared with group-raised birds. They also display

198   other behavioural problems such as impaired social skills, particularly towards mates

199   (Harvey et al., 2002). Similarly, significant between-group behavioural differences were

200   reported in young orange-winged Amazon parrots housed for a year in enriched cages,

201   either individually or with a same-sex partner (Meehan et al., 2003a). None of the pair-

202   housed parrots developed ARBs, yet 57% of the single-housed birds developed oral and/or

203   locomotor ARBs, had a more restricted behavioural repertoire, were less active and more

204   fearful: clearly demonstrating the importance of a cage-mate to the welfare of these birds

205   (Meehan et al., 2003a). From these examples, it seems clear that parental/maternal and/or

206   conspecific social contact whilst young is influential in avian behavioural development,

207   including that of ARB.

208   *2.1.3.2 Previous housing conditions*

209   The experience of pecking or foraging opportunities during early life influences FP

210   development in adult laying hens. For example, housing chicks on litter has been repeatedly

211   shown to reduce FP or its effects at adulthood (Blokhuis and van der Haar, 1989; Bestman

212   et al., 2009; Tahamtani et al., 2016), with even a short experience of litter protective against

213   FP development to some degree (10 days: Nicol et al., 2001). Scattering grain in the litter

214   (Blokhuis and van der Haar, 1992) and providing straw and objects to encourage pecking

215   during rear can result in less FP when birds are older (notably, severe FP in turkeys,

216   *Meleagris gallopavo*: Martrenchar et al., 2001). In these examples, lack of appropriate

217   foraging and exploratory opportunities and/or other stimuli during rear may result in

218 redirection of pecks towards flock-mates' feathers (*e.g.* Martrenchar et al., 2001; Bestman et

219 al., 2009).

220 Experiencing and consuming loose feathers in the rearing environment may be a key risk

221 factor for severe FP in laying hens. Hens moult three times during rear, so loose feathers are

222 plentiful (Appleby et al., 1992). However, a relative shortage of loose feathers is then

223 experienced during lay, resulting in pecking attention being redirected towards feathers still

224 attached to flock-mates (McKeegan and Savory, 1999; Ramadan and von Borell, 2008). By

225 regularly removing feathers from the rearing environment, Ramadan and von Borell (2008)

226 demonstrated that hens who do not experience plentiful loose feathers during development

227 are less likely to develop severe FP. Therefore, for laying hens 'learning' to peck at feathers

228 when young seems a key developmental step for FP at later life.

229 *2.2 Causation*

230 The causation of behaviour or, as preferred by some, mechanism of control (Bateson and

231 Laland, 2013) refers to internal and external stimuli triggering its performance. For internal

232 triggers, we include the effects of neurotransmitters, hormones, brain function, and

233 comorbidity with medical conditions. The current environment can be an external trigger for

234 ARB, but separating out the effects of current and previous environments is problematic,

235 though not a problem unique to ARB (Tinbergen, 1963; Bateson and Laland, 2013). To this

236 end, ARB can be a 'scar' of welfare problems past and not necessarily indicative of the

237 animal's current environment and welfare (*sensu*: Mason and Latham, 2004). To deal with

238 this, we have limited ourselves in all but one example (Section 2.2.4.1) to discussing clear

239 current environmental triggers for ARB.

2.2.1 Internal triggers for ARB

2.2.1.1 Neurotransmitters

The neurotransmitters dopamine (DA) and serotonin (5-hydroytryptamine, 5-HT), act in the direct and indirect neural pathways responsible for behaviour modulation (reviewed by: Garner, 2006), and are linked with ARB. Generally, ARBs are reduced through activation of the indirect or suppression of the direct pathway, demonstrated experimentally by administration of dopaminergic and serotonergic drugs (Langen et al., 2011). For instance, apomorphine, a D_1 and D_2 receptor agonist (van Hierden et al., 2005) induced object-pecking in male Japanese quail, *Coturnix japonica* (Castagna et al., 1997), and male laying chicks (Machlis, 1980), while Kjaer et al. (2004) reduced FP in laying hens with haloperidol, a D_2 receptor antagonist. Similarly, a 5-HT_{1A} receptor agonist that reduces 5-HT synthesis increased severe FP in high FP line laying chicks (also see Section 2.2.1.2: van Hierden et al., 2004a), whereas dietary supplementation of a 5-HT precursor, tryptophan, stimulated serotonergic neurotransmission and reduced FP in young laying chickens (Savory, 1998; Savory et al., 1999; van Hierden et al., 2004b). Finally, dependent upon the drug used and receptor affected, oral ARBs in broiler breeders – the parent stock of meat chickens – were either suppressed or induced with various 5-HT_{1A}, 5-HT_2 and 5-HT_3 receptor agonists and antagonists (Koštál and Savory, 1995). Altogether, increased DA activity is associated with increased ARB, but the relationship between ARBs and 5-HT function seems complex and receptor-specific, perhaps reflective of interactions between the two systems (*sensu*: Langen et al., 2011).

Neurotransmitter deficiencies are also suggested to be causal in FDB in parrots (van Zeeland et al., 2009), but experimental studies confirming this are lacking. Limited reduction in FDB using DA and 5-HT antagonist drugs do provide some cautious, anecdotal support for this (though sample sizes were small, two and 12 birds, respectively: Iglauer and Rasim,

12

265   1993; Mertens, 1997). Rigorous experimental research is therefore now required to

266   investigate relationships between DA, 5-HT and FDB.

267   *2.2.1.2 Neurotransmitters and interaction with stress response style*

268   As mentioned in Section 2.1.2.2, proactive animals are suggested to be predisposed to ARB

269   development due to response style-specific differences in 5-HT and DA activity (Koolhaas et

270   al., 1999; Ijichi et al., 2013) and sensitivity to manipulations of these systems (van Hierden,

271   2003). In line with this, proactive high FP laying chicks were more sensitive to the effects of

272   a D_1 and D_2 receptor agonist (measured by increased hyperactive locomotion) (van Hierden

273   et al., 2005). More support comes from a study that increased severe FP in high FP laying

274   chicks by reducing 5-HT synthesis with a 5-HT$_{1A}$ receptor agonist, yet observed no effect in

275   low FP chicks (van Hierden et al., 2004a). Similarly, a significant reduction of gentle FP via

276   dietary tryptophan supplementation was only found in high FP laying chicks (van Hierden et

277   al., 2004b). The predicted relationship between response style (based on FP) and 5-HT and

278   DA activity is not unequivocal, however. Variation is observed across life-stages (Buitenhuis

279   et al., 2006; Kops, et al., 2017) and across different lines (*i.e.* whether purposefully

280   selectively bred based on FP (Kops et al., 2017), or not (van Hierden et al., 2002b)), leaving

281   the response style – ARB relationship a little unclear.

282   *2.2.1.3 Hormones*

283   The onset of lay in laying hens is a key time in FP; experimental manipulation of

284   progesterone and oestrogen demonstrates the influence of these hormones (Hughes, 1973).

285   12-week old pullets received sex hormone releasing implants with un-implanted pullets used

286   as controls (Hughes, 1973). By 18 weeks, progesterone and oestrogen together resulted in a

287   large increase in FP, progesterone alone induced a lesser, but still significant, increase, and

288   the usual dramatic onset of lay increase in FP was suppressed with testosterone

289   administration from 18-24 weeks (Hughes, 1973). Given similarities in outward forms of FP

290 and FDB and the female-bias (Garner et al., 2006; Mellor, 2014) it is reasonable to predict

291 FDB may be similarly affected by hormonal control, a testable hypothesis.

292 *2.2.1.4 Nutrient deficiencies and hunger*

293 In laying hens, deficiencies in certain nutrients trigger exploratory behaviour, including

294 pecking. These deficiencies are therefore implicated in FP (Kjaer and Bessei, 2013). This

295 has been extensively reviewed elsewhere (*e.g.* van Krimpen et al., 2005; Kjaer and Bessei,

296 2013) so, aside from fibre, only a brief overview is provided here. Deficiencies in crude

297 protein (*e.g.* Ambrosen and Petersen, 1997) and specific amino acids such as methionine

298 (*e.g.* Harms and Russell, 1996; Elwinger et al., 2008), arginine (*e.g.* Sirén, 1963), and lysine

299 (*e.g.* Quentin et al., 2005) have been linked to FP, which is quickly and effectively reduced

300 when appropriate diets are fed (Kjaer and Bessei, 2013). Fibre positively affects gut motility,

301 and increases satiety levels (Hetland et al., 2004; Rodenburg et al., 2013); inadequate

302 provision of fibre is associated with severe FP (van Krimpen et al., 2009; Rodenburg et al.,

303 2013). Ingested feathers act on the gut in a similar fashion to fibre, thus by consuming

304 feathers birds may increase satiety (Harlander-Matauschek et al., 2006b). Interestingly, the

305 morphology of severe FPs (though not gentle FPs) is similar to foraging pecks, indicating the

306 likely motivational basis of severe FP (Dixon et al., 2008). FP followed by feather-eating,

307 therefore, may allow the birds to meet a dietary and digestive need not provided by the diet

308 (Rodenburg et al., 2013).

309 While FP is more commonly reported in laying strains, it is also reported in broiler breeders

310 (de Jong and Guémené, 2011) and relates to hunger (Morrissey et al., 2014a). Strong

311 artificial selection in broilers means birds can effectively reach slaughter weight through

312 rapid weight gain; this weight gain and subsequent obesity damages long-term health and

313 productivity of broiler breeders, especially females (Richards et al., 2010). To avoid this,

314 broiler breeders are usually restricted to 25-50% of *ad libitum* intake (Savory et al., 1993;

315 Renema et al., 2007), show signs of chronic hunger (Mench, 2002), and physiological

316 indications of stress, indicating that such restriction is detrimental to welfare (*e.g.* Hocking et

317 al., 1993; de Jong et al., 2002). Furthermore, feed-restriction and hunger are associated with

318 FP and oral ARBs such as spot-pecking (Sandilands et al., 2006; D'Eath et al., 2009;

319 Nielsen et al., 2011; Morrissey et al., 2014a; Morrissey et al., 2014b). To reduce hunger and

320 improve welfare, studies have investigated the effects of 'alternative' diets. Alternative diets

321 are typically qualitative-restrictive (high volume, low quality and energy) diets, prolonging

322 feeding times, and/or contain appetite suppressants (*e.g.* calcium propionate) to reduce

323 feeding motivation (*e.g.* Sandilands et al., 2006). These alternative diets are often, though

324 not always, associated with positive behavioural indicators of welfare such as a reduction in

325 FP and its effects, and more 'normal' foraging behaviour overall (reviewed by: Tolkamp and

326 D'Eath, 2016). For example, Morrissey et al., 2014a; 2014b found feather condition was

327 better in hens fed alternative compared with control diets. However, alternative diets are

328 controversial due to uncertainties surrounding their welfare effects and whether underlying

329 'metabolic hunger' for nutrients and energy is actually satisfied (see: Tolkamp and D'Eath,

330 2016).

2.2.2 Medical conditions and ARBs

332 ARB is co-morbid with some avian medical conditions. *Escherichia coli* infections (Brunberg

333 et al., 2016), intestinal worm related mortality rates, infectious bronchitis, and egg peritonitis

334 are linked with FP in laying hens (Pötzsch et al., 2001). As damaged feathers can be visual

335 cues for FP (Hughes, 1985; McAdie and Keeling, 2000), perhaps in some of these examples

336 the altered appearance (including feathers) and behaviour of ill birds has a likewise effect. In

337 parrots, FDB may coincide with endoparasite (*e.g. Giardia psittaci*, an intestinal protozon:

338 Clyde and Patton, 1996; Doneley, 2009) and ectoparasite infections (*e.g.* quill mites,

339 *Syringophilus* spp. Doneley, 2009), presumably irritating the skin and/or feathers, causing

340 the bird to chew at or remove them. This is also the case with painful and/or irritating

341 diseases (renal and liver disease: Jaensch, 2000; Burgos-Rodríguez, 2010; van Zeeland

15

342 and Schoemaker, 2014). In these instances, FDB may be localised to the painful area (*e.g.*

343 in the synsacrum in parrots with renal disease: Burgos-Rodríguez, 2010), or generalised

344 (van Zeeland and Schoemaker, 2014).

345 It should be noted that the examples given here are correlative and, in some cases,

346 anecdotal only, *i.e.* causation cannot be inferred. There could be causal mechanism linking

347 ill-health and ARB, or poor environmental conditions may be the underlying causal factor for

348 both. Experimental manipulations may aide this distinction. By experimentally administering

349 young laying hens with an immune challenge, Parmentier et al., (2009) showed a link

350 between feather condition and immune response. Poorer plumage condition, and thus

351 increased FP, was found in hens given a higher dose of human serum albumin, showing that

352 an immune response alone is sufficient to trigger FP. While the precise causal link between

353 immune response and FP was unclear, it neatly demonstrated the immune challenge itself

354 was the influencing factor, providing clear direction for further work. In all these cases,

355 however, if an ARB is just a symptom of disease, we would predict that successful disease

356 treatment would also eliminate the ARB.

357 *2.2.3 CNS dysfunction and ARBs*

358 Altered brain function and physiology is associated with ARBs in various mammalian

359 species, being best studied in humans (reviewed by: Garner, 2006), and is likewise

360 suggested to be influential in some avian ARBs. ARB-related CNS dysfunction in birds can

361 be assumed by analogy with known CNS dysfunction-induced behaviour problems in

362 humans. Similarities between FDB and trichotillomania (plucking of hair) in humans for

363 instance implies, as per trichotillomania, that CNS dysfunction underlies FDB (Moon-Fanelli

364 et al., 1999; Garner et al., 2006). CNS dysfunction is also inferred experimentally, typically,

365 by measuring perseveration. Perseveration – the inappropriate repetition of an ineffectual

366 response – is used as a proxy for CNS dysfunction, because it may indicate problems with

16

367   basal ganglia and other brain regions responsible for behaviour selection and control

368   (Norman and Shallice, 1986; Garner, 2006). Perseveration positively correlated with ARB in

369   orange-winged Amazon parrots (Garner et al., 2003b), blue tits, *Cyanistes caeruleus*, and

370   marsh tits, *Poecile palustris*, (Garner et al., 2003a), and, although less definitively, in high FP

371   laying hens (during an extinction learning task: Harlander-Matauschek et al., 2006a, but see:

372   Kjaer et al., 2015).

373   Thus when perseveration is measured, overall, it does covary with ARB in birds, *i.e.* those

374   performing the most ARB are the most perseverative. However, perseveration or

375   perseverative tendencies are also linked to stress response style (*sensu*: Koolhaas et al.,

376   1999; Coppens et al., 2010). The routine formation tendency of proactive individuals is due

377   to non-pathological individual differences in brain structure (Coppens et al., 2010). Given

378   that high FP laying hens tend to be proactive (Blokhuis and Beutler, 1992; van Hierden et al.,

379   2002a; van Hierden et al., 2002b), if these hens are more perseverative than low FP hens, is

380   this just a by-product of their response style? Or a sign of a dysfunctional CNS? More

381   damningly, in humans at least, perseveration is also seen in 'normal' individuals without

382   ARBs (*e.g.* Ramage et al., 1999). Therefore, it is unclear whether perseveration is a valid

383   proxy of brain dysfunction in avian species.

384   ## *2.2.4 Environmental triggers for ARB*

385   Many environmental risk-factors have been identified for avian ARBs, but the causal

386   connection between the trigger and the ARB is generally unknown.

387   Firstly, ARB may be triggered by discrete events. Pacing, for example, was induced in

388   Japanese quail when novel objects were placed into the cage (Saint-Dizier et al., 2008).

389   Likewise, and unexpectedly as prior to this only wild-caught birds had been reported to

390   somersault, somersaulting was triggered in hand-reared starlings during an experiment

391   investigating the potential enriching effects of videos of landscapes (Coulon et al., 2014).

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392　Similarly, the removal of a preferred environment can trigger ARB. For instance, a move

393　from large, group-housed aviaries into small single-occupancy cages quickly led to

394　somersaulting in starlings and mild FDB in an African grey parrot (Feenders and Bateson,

395　2012; van Zeeland et al., 2013a). Negative contrast effects may play a role here too (*sensu:*

396　Burman et al., 2008); for example, layer pullets switched from wood-shavings to slatted

397　floors performed more FP than those housed on slatted floors throughout (Blokhuis and

398　Arkes, 1984). It seems likely, given that ARBs were triggered so quickly in these examples,

399　that the birds found these events aversive.

400　Frustrated motivation of species-specific behaviours can lead to ARB. Here, when the

401　opportunity to perform the frustrated behaviour is provided, ARB should be reduced or even

402　eliminated (Mason and Latham, 2004). For example, water for bathing is important to duck

403　welfare (Jones et al., 2009), as illustrated by Riber and Mench (2008) who found FP was

404　higher in farmed Muscovy ducklings, *Cairina moschata*, without water access than those

405　with. Frustrated foraging motivation is often proposed to underlie oral ARBs and FDB

406　(Meehan et al., 2003b; van Zeeland et al., 2009). Supporting this are reports of increased

407　foraging times and reduced oral ARBs and FDB in canaries, *Serinus canaria domestica*, and

408　African grey parrots, respectively, using foraging enrichments (Keiper, 1969; Lumeij and

409　Hommers, 2008; van Zeeland et al., 2013a). More evidence comes from orange-winged

410　Amazon parrots, as enrichment provision reduced the amount of ARB performed

411　(unenriched birds performed more), but also changed the primary *form* of ARB (Meehan et

412　al., 2004). Enriched birds performed predominantly locomotor ARBs, whereas the mix of

413　locomotor and oral ARBs was more equal in unenriched birds (Meehan et al., 2004).

414　Interestingly, in the latter group this changed when enrichment was later provided; locomotor

415　ARBs became predominant in these birds too, implying the parrots' foraging 'needs' were

416　almost completely satisfied by the added enrichments (Meehan et al., 2004). Note that while

417　frustration would appear the most likely trigger in these examples, as ever, without careful

418　experimentation we cannot state that other causal factors were not influential.

419   Finally, housing animals – including humans – in impoverished conditions can impair CNS

420   development, causing dysfunction (Leipoldt, 1992; Lewis et al., 2006) and ARB (Hediger,

421   1950; Morris, 1964; Carlstead, 1998). Such conditions are regularly cited as causal in avian

422   ARBs (Keiper, 1969; 1970; Jacobs et al., 1995; El-Lethey et al., 2000). Small and/or

423   unenriched cages across numerous species are associated with increased ARBs, such as

424   hopping in zebra finch, *Taeniopygia guttata* (Jacobs et al., 1995), oral ARBs in budgerigars,

425   *Melopsittacus undulates* (Polverino et al., 2015), and route-tracing in canaries, (Keiper,

426   1969). Similarly, in young orange-winged Amazon parrots barren, unenriched cages reliably

427   trigger FDB and other ARBs, which are successfully reduced with provision of physical and

428   foraging enrichments (Meehan et al., 2003b; Meehan et al., 2004; Cussen and Mench,

429   2015). As the orange-winged Amazon parrots' ARBs were so easily reduced it seems

430   unlikely that CNS dysfunction was an important causal factor; a hallmark of ARB driven by

431   CNS dysfunction is that changing to more appropriate environmental conditions is unlikely to

432   alter ARB (and may even make it worse) (reviewed by: Mason and Latham, 2004). Indeed,

433   to the best of our knowledge just one study to date on laying hens has investigated the

434   effects of different housing conditions on brain development. Patzke et al., (2009) reported

435   only minor differences in key brain areas believed to be sensitive to environmental

436   stimulation: hippocampal structures and the nidopallium caudolaterale. This somewhat

437   unexpected result could indicate the adult avian brain may be less responsive to effects of

438   environmental conditions than is that of young birds (*e.g.* Leitner and Catchpole, 2007;

439   Patzke et al., 2009). However, as all the hens shared similar, possibly traumatic, pre-study

440   rearing conditions, *i.e.* non-brooded, conditions known to affect behaviour (Edgar et al.,

441   2016) and brain development (Nordquist et al., 2014) this early experience may have

442   influenced early brain development across all hens and thus explain their results (Patzke et

443   al., 2009). Therefore, this leaves plenty of scope to thoroughly investigate the effects of

444   impoverished housing conditions on CNS development and ARB in birds across life-stages.

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2.2.4.1 Flight restriction and ARB

446   Here, we detail one example where causation has not been adequately established, yet, we

447   feel its implications for avian welfare warrants discussion. Two studies using survey data

448   found various psittacine species to be at increased risk of FDB if unable to fly (pet African

449   grey parrots (Schmid et al. 2006); preliminary results from 23 pet psittacine species (Mellor,

450   2014)). Causation cannot be inferred from these examples, but the results are intriguing as

451   captive flight-adapted species often have their flight restricted or entirely prevented in

452   captivity (van Hoek and Ten Cate, 1998; Hesterman et al., 2001). Indeed, partial wing-

453   amputations did not diminish great-mynahs, *Acridotheres grandis*, preferences for large

454   spaces with vertical height, implying the birds were still motivated to fly, even if not physically

455   able (Peng et al., 2013). Preventing flight in captive birds may, therefore, represent a

456   significant area of avian welfare concern.

457   *2.3 Evolution*

458   To understand the evolution of behaviour, Tinbergen (1963) advocated comparing the

459   behaviour across a group related of species, and investigating the genetic control of species-

460   specific behaviours. In this section, therefore, interspecific differences in ARB and heritability

461   and genetics of ARB will be discussed.

462   *2.3.1 Inter-specific differences in ARB*

463   Phylogenetic comparative methods (PCMs) are useful in studying the evolution of behaviour,

464   examining how it differs across a group of species and its co-evolution with other aspects of

465   species biology and behaviour (Blumstein and Fernández-Juricic, 2010). In captive wild

466   animal welfare studies, PCMs can be used to identify species-level risk-factors (*i.e.* species-

467   typical traits) for poor captive welfare, including ARB (Clubb and Mason, 2003; Clubb and

468   Mason, 2007; Müller et al., 2011; Pomerantz et al., 2013; Kroshko et al., 2016; reviewed by:

469   Mason, 2010).

470   Currently, McDonald Kinkaid (2015) has performed the only avian welfare PCM study,

471   uncovering two risk-factors for poor welfare in parrots. Species with naturally effortful

472   foraging modes, *e.g.* Ducorp's corella, *Cacatua ducorpsii*, were at increased risk of FDB

473   (McDonald Kinkaid, 2015). The second risk-factor was relative brain volume; species with

474   relatively large brains, *e.g.* red-shouldered macaws, *Diopsittaca nobilis*, were at increased

475   risk of oral and locomotor ARBs (McDonald Kinkaid, 2015).

476   *2.3.2. Intra-specific differences in ARB*

477   *2.3.2.1 Heritability*

478   Selective breeding in laying hens demonstrates a possible heritable component to FP (*e.g.*

479   Kjaer et al., 2001). FP heritability estimates (h^2) range from 0.07 – 0.54 (Cuthbertson, 1980;

480   Bessei, 1984; Kjaer and Sørensen, 1997), and vary further between different breeds and

481   lines (Faure et al., 2003). These estimates are somewhat confounded by the fact that social

482   environment, *i.e.* flock mates, may also play a role in accurately estimating heritability for FP

483   damage (Brinker et al., 2014). In addition, many studies aggregate data on *both* types of FP

484   in their heritability estimates. This could be an important distinction to make, for Rodenburg

485   et al. (2003) found while gentle FP was heritable in their study (h^2 at 5 weeks of age = 0.12;

486   at 30 weeks = 0.15), severe FP was not. Therefore, assuming the two forms of FP really do

487   represent two distinct behaviours, establishing the heritability of each and how this varies

488   between life-stages is important.

489   Within a laboratory colony of orange-winged Amazon parrots, the h^2 estimate for FDB was

490   1.14 ± 0.27 (S.E.) (Garner et al., 2006). The estimate is greater than 1 as the small sample

491   size featured full-siblings, limiting its generalisability; replication is now required with a larger,

492   less related sample (van Zeeland et al., 2009). However, this does suggest, as with laying

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493   hens, it might be possible to select against FDB (Garner et al., 2006). Heritability of

494   locomotor and oral ARBs in this study was low: h^2 = -0.08 ± 0.14, though it is possible that

495   the close relatedness, and thus little genetic variability, within their study group may explain

496   this (Garner et al., 2006).

497   *2.3.2.2 Genes*

498   Molecular research has identified several genomic regions associated with FP. In adult

499   laying hens possible quantitative trait loci (QTL), and clues of the likely location of genes for

500   performing gentle and severe FP, were found on chromosome GGA2, and a potential one

501   for receiving gentle FP on GGA5 (Buitenhuis et al., 2003a; 2003b). QTL locations for FP

502   differed in 6-week old chicks though, performing gentle FP was located on GGA10, receiving

503   gentle FP on GGA1, alongside further suggestive QTL on GGA2, 6, and 7 (Buitenhuis et al.,

504   2003a). Biscarini et al. (2010) found good agreement with these QTL mapping studies,

505   uncovering associations between giving and receiving FPs and single-nucleotide

506   polymorphisms (SNPs) on many of the same chromosomes (see: Buitenhuis et al., 2003a;

507   2003b).

508   Specific gene-expression relates to FP. By comparing the genetic profiles of high and low FP

509   laying hens, Flisikowski et al., (2009) uncovered two candidate genes associated with FP:

510   DRD4 and DEAF1. These respectively encode for DA receptor D_4 and a 5-HT regulatory

511   factor. Emerging evidence also suggests that some high FP laying hens show hyperactivity-

512   type behaviour (Kjaer, 2009; Labouriau et al., 2009), perhaps underpinned by higher DA

513   activity and thus a more active motor-system output overall (Kops et al., 2017). While the

514   sample size was very small, Labouriau et al. (2009) reported differences in gene expression

515   between the hyperactive high FPs (N = 4) and more 'normal' birds (N = 56), notably OPRD1

516   and OPRK, which relate to the opioid system (Labouriau et al., 2009). As well as these links

517   to DA and 5-HT systems, FP is associated with genes directly and indirectly involved in

518   absorption of nutrients from the intestine, glucose homeostasis, and the immune system

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519   (Biscarini et al., 2010; Brunberg et al., 2011). Causal links between these genes and FP

520   cannot be inferred from these studies, but they do further strengthen proposed relationships

521   between FP and feeding motivation, and the DA and 5-HT systems.

522   Finally, research into the genetic profile of FP *victims* using white leghorn and red jungle fowl

523   crosses, revealed a gene for feather pigmentation, PMEL17, predicted the severity of feather

524   damage (Keeling et al., 2004). The white leghorn's dominant white allele (I) inhibits feather

525   pigmentation, the wild-type recessive allele (i) results in some degree of feather

526   pigmentation. Thus, recessive homozygotes (i/i) received the most FP damage, dominant

527   homozygotes (I/I) the least, with heterozygotes (I/i) intermediate (Keeling et al., 2004).

528   Wood-shavings in the litter were suggested to be more conspicuous on the feathers of

529   pigmented birds, serving as a pecking stimulus (Keeling et al., 2004).

2.4 Function

531   In this section, the function of behaviour is considered. Generally speaking, behaviours

532   increase the fitness of the individual, be it through increasing immediate survivorship, or

533   reproductive output (*sensu*: Tinbergen, 1963). Where do ARBs fit into this? Common

534   definitions of ARB emphasise its seemingly 'functionless' nature (Ödberg, 1978; Wiepkema,

535   1983); in some cases it is very difficult to see how ARBs serve to benefit the animal, *e.g.*

536   self-damaging ARBs such as FDB leading to skin damage and infection (Meehan et al.,

537   2003b; van Zeeland et al., 2009). However, combining evidence from better-studied taxa

538   with a limited quantity of avian research, here we discuss potential functions of some specific

539   cases of ARB, as well as considering cases where ARB may be functionless.

2.4.1 ARB and coping

541   ARB may calm an animal or facilitate coping with stressors. Firstly, ARB may reduce

542   physiological stress (*e.g.* self-injurious biting in primates reduces heart rate: Novak, 2003), or

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543   alleviate signs of pain (*e.g.* crib-biting provides gastric irritation relief to horses: Wickens and

544   Heleski, 2010), and is implied in FDB in parrots with renal disease (Burgos-Rodríguez,

545   2010). Additionally, ARB can be self-reinforcing ('DIY enrichments') and, as reported by

546   humans, repetition itself is stress-relieving ('mantra effects') (Mason and Latham, 2004),

547   allowing a regain of control and reduction in anxiety, especially after a stressful event (Eilam

548   et al., 2011; Lang et al., 2015). When an ARB allows an animal to cope, in the Tinbergian

549   sense "... the animal would be worse off if deprived of this attribute." (Tinbergen, 1963), ARB

550   is thus associated with an improvement in welfare when the behaviour is performed (*sensu*:

551   Mason and Latham, 2004).

552   Though 'coping' is widely suggested to underlie several avian ARBs (*e.g.* in conures,

553   *Pyrrhura perlata perlata*: van Hoek and King, 1997), to the best of our knowledge, this has

554   never been formally tested. We do, however, have two tentative potential avian coping

555   examples. The first relates to FP, and eating, caused by low fibre diets in laying hens (van

556   Krimpen et al., 2009), whereby birds could be coping by managing a dietary and digestive

557   need not provided by the diet (see Section 2.2.1.4). Our second 'coping' example is FDB

558   associated with a painful disease: *e.g.* in parrots with renal disease (see Section 2.2.2)

559   (Burgos-Rodríguez, 2010). In humans, stimulating certain areas of the body reduces pain via

560   endorphin release (termed acupuncture analgesia), in itself a reinforcing act (Wang et al.,

561   2008). Self-harming humans and self-biting rhesus macaques target many of the same

562   body areas (Wisely et al., 2002; Polanco, 2016). It is not implausible that FDB in this

563   instance could be a do-it-yourself pain relief to alleviate disease-related pain.

564   Clearly, these hypotheses require testing, and the multi-factorial nature of FP and FDB

565   means they may be coping mechanisms only under these very specific circumstances. We

566   would predict, however, if ARB does allow the animal to cope, that indicators of improved

567   welfare would be seen, such as decreased indications of hunger post-feather consumption

568   by laying hens, and reductions in arousal, such as heart rate, during and immediately after a

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569   bout of FDB (based on: Novak, 2003), and that prevention of the ARB would negatively

570   impact welfare (Mason and Latham, 2004).

2.4.2 ARB and CNS dysfunction

572   Finally, ARB may be indicative of an animal and its brain having been permanently altered

573   by captivity. If perseveration is indicative of CNS dysfunction (but see Section 2.2.3) then in

574   the perseverative orange-winged Amazon parrots, blue tits and marsh tits we may have

575   evidence of CNS dysfunction (Garner et al., 2003a; Garner et al., 2003b). Logically we might

576   also expect CNS changes to affect overall behaviour (*sensu*: Mason and Latham, 2004).

577   Hawaiian crows may demonstrate such pervasive behavioural changes: as well as more

578   ARB, adult crows raised in social isolation as chicks showed inappropriate play and social

579   behaviour, especially towards mates, directly reducing reproductive output (Harvey et al.,

580   2002). Associations between ARB and reduced reproductive success are reported in other

581   species (American mink, *Neovison vison*: Díez-León et al., 2013). It therefore seems likely

582   that signs of behavioural abnormality alongside ARB are indicative of an animal altered by

583   captivity, with CNS pathology implicit in this. As such, for a bird with its behavioural

584   repertoire shaped and affected by such conditions, it is most unlikely that ARB serves it any

585   function.

3. Discussion and conclusions

587   This review has considered avian ARBs from Tinbergen's four interactive perspectives:

588   development, causation, evolution, and function. Throughout, we have been limited to

589   discussing a minority of representatives from this diverse taxonomic group. This does not

590   mean absence of ARB evidence in other species equates to evidence of absence; more

591   likely under- or non-reporting is the case. Given that thousands of avian species are held in

592   captivity, and that the commonest captive bird species (domestic chicken) numbers in the

593   billions, the extent of this could be far-reaching, leaving plentiful opportunities for future

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594   research. By reviewing different ARBs in the species discussed here, we hope this review

595   provides a good starting point for researchers to go forward and investigate avian ARBs

596   further, both in well-studied species and others. Below we summarise the four perspectives

597   of avian ARBs, indicating current gaps in knowledge and directions for research.

598   In relation to development, female laying hens, jungle fowl, and parrots are at higher risk of

599   FP (Jensen et al., 2005) and FDB (Garner et al., 2006; Mellor, 2014), with the onset of lay a

600   crucial time in FP (Hughes, 1973). As evidenced in high FP laying hens (*e.g.* Blokhuis and

601   Beutler, 1992) and, to a lesser extent, African grey parrots with FDB (van Zeeland et al.,

602   2013b), birds with a proactive stress response style are more susceptible to ARB, though

603   this now needs replication in other species. Studies on causation should be informed by

604   knowledge of these developmental risk-factors for ARB, *e.g.* given the female-bias future

605   studies might ask how sex hormones affect FDB. Additionally, the developmental trajectory

606   of ARB is poorly described and understood in all but two species, and biased towards

607   younger birds (*e.g.* Huber-Eicher and Sebö, 2001; Meehan et al., 2004). Therefore, this is a

608   research area requiring attention, to unpick whether certain developmental windows are key

609   to ARB at different life-stages, ARB 'treatability', and what this implies about the root

610   cause(s) of ARB.

611   The rearing environment clearly influences ARB development. Providing opportunities to

612   develop and perform highly motivated behaviours, such as foraging and environmental

613   exploration, offers at least some protection against ARBs when older (FP: Blokhuis and van

614   der Haar, 1989; Martrenchar et al., 2001; Nicol et al., 2001; Bestman et al., 2009; Tahamtani

615   et al., 2016). Appropriate parental and social contact whilst young also shapes behavioural

616   development, including ARB, in both precocial and altricial species (Harvey et al., 2002;

617   Perré et al., 2002; Meehan et al., 2003a). However, early maternal separation and hand-

618   rearing seem to be influential in ARB development in some (Schmid et al., 2006), but not all

619   species (Feenders and Bateson, 2011; 2012; 2013). As an example, Riber et al., (2007)

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620   found that brooded layer chicks pecked the ground sooner and more often than non-brooded

621   chicks. When older, brooded chicks also performed fewer severe FPs and suffered less

622   cannibalism-related mortality than non-brooded (Riber et al., 2007).

623   Experience of wild conditions may predispose some species such as European starlings

624   (Feenders and Bateson, 2012) and blue jays (Keiper, 1969) to ARB (with the caveat of

625   rearing method confounds). Typically, the opposite is reported for wild-caught mammals,

626   believed to be protected from ARB by their natural, complex upbringing (Mason, 2006a).

627   Captivity can very quickly alter the behaviour of wild-caught birds. Butler et al. (2006) found

628   time in captivity predicted behavioural responses of wild-caught chaffinches, *Fringilla*

629   *coelebs*, during a foraging task, with chaffinches held the longest least likely to forage

630   despite having lost the most weight. Furthermore, wild-caught parrots have a greater stress

631   response to an acute stressor than parent-reared and captive-bred birds (Cabezas et al.,

632   2013), and are those at highest risk of FDB (Schmid et al., 2006). This latter finding is

633   especially important, as unlike the starlings and blue jays, the origin and ARB-risk

634   relationship is not confounded by rearing technique, *i.e.* there are parent-reared captive-bred

635   parrots for comparison. Perhaps therefore for some birds, in contrast to wild-caught

636   mammals, the seemingly protective nature of a wild upbringing is outweighed by the acts of

637   removal from the wild and introduction into captivity (with confinement being especially acute

638   for an animal that usually inhabits a significant three-dimensional space). So much so, that

639   behavioural indicators of compromised welfare, including ARB and other behavioural

640   changes, quickly emerge.

641   Studies on internal causal triggers for ARB (principally in laying hens) implicate the roles of

642   neurotransmitters, especially DA (*e.g.* Kjaer et al., 2004), sex hormones (Hughes, 1973),

643   and dietary deficiencies (*e.g.* van Krimpen et al., 2007) on FP and other ARBs (*e.g.*

644   Sandilands et al., 2006). Elevated DA activity is fairly clearly related to increased ARBs, but

645   the relationship is less convincingly established between 5-HT and ARBs. Further

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646   examination of the variation in neurotransmitter–ARB relationships across life-stages (*e.g.*

647   Kops et al., 2017) is another potentially fruitful area for future studies. The relationship

648   between FP and sex hormones might be explained by changing nutritional needs of laying

649   hens – potentially in female parrots with FDB too – due to the cost of egg production during

650   lay. Energetic requirements increase at this time, and increased pecking may indicate

651   increased feeding motivation, or hunger for nutrients which feathers may provide (Jensen et

652   al., 2005). This could explain why FP is more commonly reported in laying strains of chicken,

653   with their higher levels of egg production, than it is in broiler breeders.

654   CNS dysfunction is an important cause of ARB in other species (reviewed by: Garner, 2006),

655   but it is not yet well-understood in birds. ARBs are reportedly extremely commonplace in

656   some laboratory birds (up to 84.7% of active time in orange-winged Amazon parrots: Garner

657   et al., 2006), with some evidence for CNS dysfunction (Garner et al., 2003b). Since

658   laboratory-held birds are commonly used in behavioural research (Bateson and Feenders,

659   2010), a prevalence of CNS dysfunction and ARB would undermine the scientific validity of

660   these models of 'normal' function, a matter of significant scientific concern (Garner et al.,

661   2003b).

662   The environment can trigger ARB, though it is unclear *how* ARB is caused in most cases.

663   Discrete, potentially aversive events such as moving cage (*e.g.* Feenders and Bateson,

664   2012) or removal of a preferred environment (*e.g.* Blokhuis and Arkes, 1984) can almost

665   immediately trigger ARB, as can long-term housing in impoverished conditions (*e.g.* Meehan

666   et al., 2004), and frustration of highly motivated behaviours (*e.g.* Riber and Mench, 2008). In

667   order to efficiently address ARB, it is essential to first know how environmental conditions

668   have caused the ARB. For instance, we might unnecessarily dismiss an environmental

669   change or enrichment's ability to improve welfare in birds in which irreversible CNS

670   dysfunction has already developed (reviewed by: Mason and Latham, 2004). Establishing

671   causation is therefore fundamental in effectively improving welfare.

28

672   Species' evolutionary history can result in mismatches between how the species has

673   evolved to behave and how the captive environment permits individuals to behave, resulting

674   in ARB. Broiler chickens have been artificially selected for rapid weight gain driven by high

675   feeding motivation, indeed, if permitted they eat far beyond what they require for energetic

676   homeostasis (Richards et al., 2010). Broiler breeders are feed-restricted for health reasons

677   (Richards et al., 2010), but with their high feeding motivation show signs of chronic hunger

678   (Mench, 2002), triggering ARBs (*e.g.* FP: Morrissey et al., 2014a; oral ARBs: Sandilands et

679   al. 2006; Nielsen et al., 2011). Likewise, wild parrots invest heavily in feeding and foraging

680   (Snyder et al., 1987) and their captive counterparts are likely to be similarly motivated. It is

681   perhaps unsurprising that naturally effortful foraging modes emerged as a risk-factor for FDB

682   in parrots (McDonald Kinkaid, 2015), making it clear that for some, foraging behavioural

683   needs are hard to facilitate in captivity. Thus, these evolutionary history mismatches, be it

684   through natural or artificial selection, are influential in ARB and if understood can inform how

685   best to improve welfare. To illustrate, tailoring enrichments to facilitate species-specific

686   foraging modes that are known risk-factors for FDB may help protect against FDB

687   development.

688   Flight, in species capable of flight, is one of the most constrained natural behaviours in

689   captive birds, with restricted flight associated with ARB, as detailed in Section 2.2.4.1 (*e.g.*

690   Schmid et al., 2006; Mellor, 2014). Whether negative welfare effects of flight restriction have

691   exact parallels with spatial restrictions in mammals, or if there is something special about

692   flight *per se* which when restricted in captivity compromises welfare, is unclear. To better

693   understand this, future studies could make good use of PCMs to ask whether heavily flight-

694   dependent species are at increased risk of poor captive welfare compared with those that fly

695   less or not at all.

696   There is evidence for heritability in FP in laying hens and, perhaps, FDB in parrots (*e.g.*

697   Kjaer et al., 2001; Garner et al., 2006). Based on this, it may seem logical to selectively

698   breed against ARB, however, this may be costly. To start, other traits could be inadvertently

699   selected for when selecting against ARB (for example, FP may have been accidently

700   selected for whilst breeding for improved egg-production: Nicol, 2015). In divergent lines of

701   mink based on ARB, the low ARB line were more fearful (Hansen and Jeppesen, 2006;

702   Svendsen et al., 2007). Here, selection against ARB may have resulted in selection for

703   apathy, another indication of poor welfare in itself (Fureix and Meagher, 2015). Therefore,

704   purposefully selecting against ARB based on ARB alone is unwise. Early molecular work on

705   genes associated with FP (*e.g.* Flisikowski et al., 2009; Biscarini et al., 2010; Brunberg et al.,

706   2011), should now be developed further. Ideally future studies should examine other species

707   (*e.g.* FDB and parrots) and incorporate evidence from causation studies, *e.g.* examining

708   relationships between ARB and DA and 5-HT expression.

709   Lastly, we proposed two cautious suggestions of where ARBs may provide function to a bird

710   by facilitating coping: FP and subsequent feather-eating in laying hens (*e.g.* van Krimpen et

711   al., 2009), and FDB performance associated with disease-related pain (Burgos-Rodríguez,

712   2010). However, there is also some evidence of instances where ARB may result from a

713   dysfunctional CNS (Garner et al., 2003a; Garner et al., 2003b), and is therefore unlikely to

714   be functional. As implicit in this aetiology of ARB are negative welfare effects of

715   impoverished living conditions (*e.g.* Hediger, 1950), we need to better understand how a

716   bird's environment affects CNS development.

717   Many, if not all, of the avian ARBs described here are multi-factorial behaviours with

718   complex aetiologies. Any approach taken to effectively understand and address them,

719   therefore, needs to reflect this. For example, consider FP in laying hens. In severe FP

720   *development*, the behaviour becomes more prevalent and frequent with age, particularly

721   around the onset of lay, with proactive individuals especially predisposed to FP. Chicks'

722   rearing conditions, such as 'learning' to eat loose feathers, also affect severe FP propensity

723   in later life. In terms of *causation*, manipulations of neurotransmitters and sex hormones

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724   demonstrate the internal causal roles they have on FP, while dietary deficiencies and hunger

725   are also important triggers. Considering the *evolutionary history* of FP, early artificial

726   selection for increased egg-production may have inadvertently also selected for FP, and

727   there are indications that FP may be heritable and under some degree of genetic influence.

728   The *function* of severe FP, especially if birds consume the feathers they peck, may be to

729   allow the hen to manage a nutritional need not provided by the diet. At present, severe FP is

730   often managed commercially by routine beak-trimming (though it is banned or strictly

731   controlled in some countries: van Horne and Achterbosch, 2008). However, beak-trimming is

732   painful and addresses only the immediate outcome of the behaviour. The alternative

733   approach, as evidenced in the review, is a comprehensive and multi-faceted study of the

734   ARB. For instance: how does a rearing and adult environment with plentiful foraging

735   opportunities interact with chicks being brooded to mitigate severe FP development? Can we

736   select for personality or production traits, such as low mortality rate (see: Nordquist et al.,

737   2011), that interact with these improved conditions in order to reduce FP? It is surely more

738   effective and ethical to comprehensively consider ARB from every perspective, to

739   understand and resolve the problem coherently rather than just addressing the immediate

740   outcome. One important caveat in our above example is our use of evidence from research

741   on severe FP and overall FP (*i.e.* severe and gentle FP is pooled). Unfortunately FP form is

742   not always specified in scientific papers, though they are very likely distinct behaviours with

743   differing welfare outcomes. We would therefore strongly encourage researchers to

744   discriminate between the two forms of FP wherever possible.

745   To conclude, a diverse range of ARBs are performed by birds. Thousands of avian species

746   are held in different captive settings, as pets, in zoos, as research animals, and extensively

747   in food production, so the scale of ARB and the associated poor welfare is potentially huge.

748   Employing Tinbergen's approach in investigating ARB highlights extensive gaps in our

749   current knowledge. Key areas now requiring attention are: how ARB develops and changes

750   over the course of an individual's lifetime; precisely how the environment causes ARB; a

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751 comprehensive investigation on a wide range of taxa to better understand evolutionary

752 factors; and, lastly, directed studies to determine whether or not specific ARBs provide

753 function to the performer. Finally, Tinbergen's approach emphasises the complex, multi-

754 factorial nature of ARB and, importantly, indicates how best to address them.

Conflicts of interest

756 None.

Acknowledgements

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References

772 Ambrosen, T., Petersen, V., 1997. The influence of protein level in the diet on cannibalism

773 and quality of plumage of layers. Poultry Sci. 76, 559-563.

774 Appleby, M.C., Hughes, B.O., Elson, H.A., 1992. Poultry production systems. Behaviour,

775 management and welfare. CAB international.

776 Bashaw, M.J., Tarou, L.R., Maki, T.S., Maple, T.L., 2001. A survey assessment of variables

777 related to stereotypy in captive giraffe and okapi. Appl. Anim. Behav. Sci. 73, 235-247.

778 Bateson, M., Feenders, G., 2010. The use of passerine bird species in laboratory research:

779 implications of basic biology for husbandry and welfare. ILAR J. 51, 394-408.

780 Bateson, P., Laland, K.N., 2013. Tinbergen's four questions: an appreciation and an update.

781 Trends Ecol. Evol. 28, 712-718.

782 Benhajali, H., Ezzaouia, M., Lunel, C., Charfi, F., Hausberger, M., 2014. Stereotypic

783 behaviours and mating success in domestic mares. Appl. Anim. Behav. Sci. 153, 36-42.

784 Bessei, W., 1984. Untersuchungen zur heritabilität des Federpickverhaltens bei

785 Junghennen. I. Mitteilung. Arch. Geflügelk 48, 224-231.

786 Bestman, M., Koene, P., Wagenaar, J.-P., 2009. Influence of farm factors on the occurrence

787 of feather pecking in organic reared hens and their predictability for feather pecking in the

788 laying period. Appl. Anim. Behav. Sci. 121, 120-125.

789 Biscarini, F., Bovenhuis, H., van der Poel, J., Rodenburg, T.B., Jungerius, A.P., van

790 Arendonk, J.A.M., 2010. Across-Line SNP Association Study for Direct and Associative

791 Effects on Feather Damage in Laying Hens. Behav. Genet. 40, 715-727.

33

792   Blokhuis, H., van der Haar, J., 1992. Effects of pecking incentives during rearing on feather

793   pecking of laying hens. Brit. Poultry Sci. 33, 17-24.

794   Blokhuis, H.J., Arkes, J.G., 1984. Some observations on the development of feather-pecking

795   in poultry. Appl. Anim. Behav. Sci. 12, 145-157.

796   Blokhuis, H.J., Beutler, A., 1992. Feather pecking damage and tonic immobility response in

797   two lines of White Leghorn hens. J. Anim. Sci. 70, 170.

798   Blokhuis, H.J., van der Haar, J.W., 1989. Effects of floor type during rearing and of beak

799   trimming on ground pecking and feather pecking in laying hens. Appl. Anim. Behav. Sci. 22,

800   359-369.

801   Blumstein, D.T., Fernández-Juricic, E., 2010. The Evolution of Behavior and Comparative

802   Studies, in: Blumstein, D.T., Fernández-Juricic, E. (Eds.), A Primer of Conservation

803   Behavior, Sinauer Assocites, Inc. Publishers, Sunderland, Massachusetts, pp. 31-41.

804   Bolhuis, J.E., Ellen, E.D., Van Reenen, C.G., De Groot, J., Napel, J.T., Koopmanschap,

805   R.E., De Vries Reilingh, G., Uitdehaag, K.A., Kemp, B., Rodenburg, T.B., 2009. Effects of

806   genetic group selection against mortality on behavior and peripheral serotonin in domestic

807   laying hens with trimmed and intact beaks. Physiol. Behav. 97, 470-475.

808   Brilot, B.O., Asher, L., Feenders, G., Bateson, M., 2009. Quantification of abnormal repetitive

809   behaviour in captive European starlings (*Sturnus vulgaris*). Behav. Process. 82, 256-264.

810   Brunberg, E., Jensen, P., Isaksson, A., Keeling, L., 2011. Feather pecking behavior in laying

811   hens: Hypothalamic gene expression in birds performing and receiving pecks. Poult. Sci. 90,

812   1145-1152.

34

813 Brunberg, E.I., Rodenburg, T.B., Rydhmer, L., Kjaer, J.B., Jensen, P., Keeling, L.J., 2016.

814 Omnivores Going Astray: A Review and New Synthesis of Abnormal Behavior in Pigs and

815 Laying Hens. Front. Vet. Sci. 3, 57.

816 Buitenhuis, A., Rodenburg, T., Siwek, M., Cornelissen, S., Nieuwland, M., Crooijmans, R.,

817 Groenen, M., Koene, P., Bovenhuis, H., van der Poel, J., 2003a. Identification of quantitative

818 trait loci for receiving pecks in young and adult laying hens. Poultry Sci. 82, 1661-1667.

819 Buitenhuis, A., Rodenburg, T., van Hierden, Y., Siwek, M., Cornelissen, S., Nieuwland, M.,

820 Crooijmans, R., Groenen, M., Koene, P., Korte, S., 2003b. Mapping quantitative trait loci

821 affecting feather pecking behavior and stress response in laying hens. Poultry Sci. 82, 1215-

822 1222.

823 Buitenhuis, A.J., Kjaer, J.B., Labouriau, R., Juul-Madsen, H.R., 2006. Altered circulating

824 levels of serotonin and immunological changes in laying hens divergently selected for

825 feather pecking behavior. Poultry Sci. 85, 1722-1728.

826 Burgos-Rodríguez, A.G., 2010. Avian Renal System: Clinical Implications. Vet. Clin. N. Am-

827 Exotic 13, 393-411.

828 Burman, O.H.P., Parker, R.M.A., Paul, E.S., Mendl, M., 2008. Sensitivity to reward loss as

829 an indicator of animal emotion and welfare. Biol. Lett. 4, 330-333.

830 Butler, D., Davis, C., 2010. Effects of plastic bits on the condition and behaviour of captive-

831 reared pheasants. Vet. Rec. 166, 398-401.

832 Butler, S., Whittingham, M., Quinn, J., Cresswell, W., 2006. Time in captivity, individual

833 differences and foraging behaviour in wild-caught chaffinches. Behaviour 143, 535-548.

834   Cabezas, S., Carrete, M., Tella, J.L., Marchant, T.A., Bortolotti, G.R., 2013. Differences in

835   acute stress responses between wild-caught and captive-bred birds: a physiological

836   mechanism contributing to current avian invasions? Biol. Invasions 15, 521-527.

837   Carlstead, K., 1998. Determining the causes of stereotypic behaviours in zoo carnivores:

838   towards developing appropriate enrichment., in: Shepherdson, D.J., Mellen, J., Hutchines,

839   M. (Eds.), Second Nature: Environmental Enrichment for Captive Mammals., Smithsonian

840   Institution Press, Washington DC, pp. 172-183.

841   Castagna, C., Ball, G.F., Balthazart, J., 1997. Effects of Dopamine Agonists on Appetitive

842   and Consummatory Male Sexual Behavior in Japanese Quail. Pharmacol. Biochem. Be. 58,

843   403-414.

844   Clubb, R., Mason, G., 2003. Animal Welfare: Captivity effects on wide-ranging carnivores.

845   Nature 425, 473-474.

846   Clubb, R., Mason, G.J., 2007. Natural behavioural biology as a risk factor in carnivore

847   welfare: How analysing species differences could help zoos improve enclosures. Appl. Anim.

848   Behav. Sci. 102, 303-328.

849   Clyde, V.L., Patton, S., 1996. Diagnosis, treatment, and control of common parasites in

850   companion and aviary birds, Seminars in Avian and Exotic Pet Medicine, Elsevier, pp. 75-84.

851   Conde, D.A., Flesness, N., Colchero, F., Jones, O.R., Scheuerlein, A., 2011. An Emerging

852   Role of Zoos to Conserve Biodiversity. Science 331, 1390-1391.

853   Coppens, C.M., de Boer, S.F., Koolhaas, J.M., 2010. Coping styles and behavioural

854   flexibility: towards underlying mechanisms. Philos. T. Roy. Soc. B 365, 4021-4028.

855   Coulon, M., Henry, L., Perret, A., Cousillas, H., Hausberger, M., George, I., 2014. Assessing

856   Video Presentations as Environmental Enrichment for Laboratory Birds. PLos ONE 9.

857   Cussen, V.A., Mench, J.A., 2015. The relationship between personality dimensions and

858   resiliency to environmental stress in orange-winged amazon parrots (*Amazona amazonica*),

859   as indicated by the development of abnormal behaviors. PLoS One 10, e0126170.

860   Cuthbertson, G.J., 1980. Genetic variation in feather-pecking behaviour. Brit. Poultry Sci. 21,

861   447-450.

862   Dalton, H., Wood, B., Torrey, S., 2013. Injurious pecking in domestic turkeys: development,

863   causes, and potential solutions. World's Poultry Sci. J. 69, 865-876.

864   Degen, A.A., Kam, M., Rosenstrauch, A., 1989. Time-activity budget of ostriches (*Struthio*

865   *camelus*) offered concentrate feed and maintained in outdoor pens. Appl. Anim. Behav. Sci.

866   22, 347-358.

867   D'Eath, R.B., Tolkamp, B.J., Kyriazakis, I., Lawrence, A.B., 2009. 'Freedom from hunger'

868   and preventing obesity: the animal welfare implications of reducing food quantity or quality.

869   Anim. Behav. 77, 275-288.

870   de Jong, I.C., Guémené, D., 2011. Major welfare issues in broiler breeders. World's Poultry

871   Sci. J. 67, 73-82.

872   de Jong, I.C., Voorst, S.V., Ehlhardt, D.A., Blokhuis, H.J., 2002. Effects of restricted feeding

873   on physiological stress parameters in growing broiler breeders. Brit. Poultry Sci. 43, 157-

874   168.

875   Díez-León, M., Bowman, J., Bursian, S., Filion, H., Galicia, D., Kanefsky, J., Napolitano, A.,

876   Palme, R., Schulte-Hostedde, A., Scribner, K., 2013. Environmentally enriched male mink

877   gain more copulations than stereotypic, barren-reared competitors. PLoS One 8, e80494.

878   Dixon, L.M., Duncan, I.J.H., Mason, G., 2008. What's in a peck? Using fixed action pattern

879   morphology to identify the motivational basis of abnormal feather-pecking behaviour. Anim.

880   Behav. 76, 1035-1042.

881   Doneley, R.J., 2009. Bacterial and parasitic diseases of parrots. Vet. Clin. N. Am.-Exotic 12,

882   417-432.

883   Duncan, I.J.H., Wood-Gush, D.G.M., 1972. Thwarting of feeding behaviour in the domestic

884   fowl. Anim. Behav. 20, 444-451.

885   Edgar, J., Held, S., Jones, C., Troisi, C., 2016. Influences of Maternal Care on Chicken

886   Welfare. Animals 6, 2.

887   Eilam, D., Izhar, R., Mort, J., 2011. Threat detection: Behavioral practices in animals and

888   humans. Neurosci. Biobehav. R. 35, 999-1006.

889   El-Lethey, H., Aerni, V., Jungi, T., Wechsler, B., 2000. Stress and feather pecking in laying

890   hens in relation to housing conditions. Brit. Poultry Sci. 41, 22-28.

891   Elwinger, K., Tufvesson, M., Lagerkvist, G., Tauson, R., 2008. Feeding layers of different

892   genotypes in organic feed environments. Brit. Poultry Sci. 49, 654-665.

893   FAO, 2014. FAOSTAT: Number of layer hens and broilers produced worldwide in 2014.

894   http://www.fao.org/faostat/en/#data/QL *accessed 16/08/2017*

895   Faure, J., Bessei, W., Jones, R., 2003. Direct Selection for Improvement of Animal Well-

896   being. Poultry Genetics, Breeding, and Biotechnology, pp. 221-245.

897   Feenders, G., Bateson, M., 2011. Hand-rearing reduces fear of humans in European

898   starlings, *Sturnus vulgaris*. PLoS One 6, e17466.

899   Feenders, G., Bateson, M., 2012. The development of stereotypic behavior in caged

900   European starlings, *Sturnus vulgaris*. Dev. Psychobiol. 54, 773-784.

901   Feenders, G., Bateson, M., 2013. Hand rearing affects emotional responses but not basic

902   cognitive performance in European starlings. Anim. Behav. 86, 127-138.

903   Flisikowski, K., Schwarzenbacher, H., Wysocki, M., Weigend, S., Preisinger, R., Kjaer, J.B.,

904   Fries, R., 2009. Variation in neighbouring genes of the dopaminergic and serotonergic

905   systems affects feather pecking behaviour of laying hens. Anim. Genet. 40, 192-199.

906   Fureix, C., Meagher, R.K., 2015. What can inactivity (in its various forms) reveal about

907   affective states in non-human animals? A review. Appl. Anim. Behav. Sci. 171, 8-24.

908   Garner, J.P., 2006. Perseveration and Stereotypy - Systems-level Insights from Clinical

909   Psychology, in: Mason, G., Rushen, J. (Eds.), Stereotypic Animal Behaviour: Fundamentals

910   and Applications to Welfare, CABI, Oxfordshire, UK, pp. 121-152.

911   Garner, J.P., Mason, G.J., 2002. Evidence for a relationship between cage stereotypies and

912   behavioural disinhibition in laboratory rodents. Behav. Brain Res. 136, 83-92.

913   Garner, J.P., Mason, G.J., Smith, R., 2003a. Stereotypic route-tracing in experimentally

914   caged songbirds correlates with general behavioural disinhibition. Anim. Behav. 66, 711-727.

915   Garner, J.P., Meehan, C.L., Famula, T.R., Mench, J.A., 2006. Genetic, environmental, and

916   neighbor effects on the severity of stereotypies and feather picking in Orange-winged

917   Amazon parrots (*Amazona amazonica*): An epidemiological study. Appl. Anim. Behav. Sci.

918   96, 153-168.

919   Garner, J.P., Meehan, C.L., Mench, J.A., 2003b. Stereotypies in caged parrots,

920   schizophrenia and autism: evidence for a common mechanism. Behav. Brain Res. 145, 125-

921   134.

39

922   Gaskins, L.A., Bergman, L. , 2011. Surveys of avian practitioners and pet owners regarding

923   common behavior problems in psittacine birds. J. Avian Med. Surg. 25, 111-118.

924   Gentle, M.J., Waddington, D., Hunter, L.N., Jones, R.B., 1990. Behavioural evidence for

925   persistent pain following partial beak amputation in chickens. Appl. Anim. Behav. Sci. 27,

926   149-157.

927   Gilani, A.-M., Knowles, T.G., Nicol, C.J., 2013. The effect of rearing environment on feather

928   pecking in young and adult laying hens. Appl. Anim. Behav. Sci. 148, 54-63.

929   Glatz, P., 2000. Effect of declawing on behavior of farmed emus. Asian Austral J. Anim. 14,

930   288-296.

931   Glatz, P.C., Murphy, L., Reston, A., 1992. Analgesic therapy of beak-trimmed chickens.

932   Aust. Vet. J. 69, 18-18.

933   Gustafson, L.A., Cheng, H.-W., Garner, J.P., Pajor, E.A., Mench, J.A., 2007. Effects of bill-

934   trimming Muscovy ducks on behavior, body weight gain, and bill morphopathology. Appl.

935   Anim. Behav. Sci. 103, 59-74.

936   Hansen, S.W., Jeppesen, L.L., 2006. Temperament, stereotypies and anticipatory behaviour

937   as measures of welfare in mink. Appl. Anim. Behav. Sci. 99, 172-182.

938   Harlander-Matauschek, A., Baes, C., Bessei, W., 2006a. The demand of laying hens for

939   feathers and wood shavings. Appl. Anim. Behav. Sci. 101, 102-110.

940   Harlander-Matauschek, A., Piepho, H., Bessei, W., 2006b. The effect of feather eating on

941   feed passage in laying hens. Poultry Sci. 85, 21-25.

942   Harms, R., Russell, G., 1996. A re-evaluation of the methionine requirement of the

943   commercial layer. J. Appl. Anim. Res. 9, 141-151.

40

944 Harvey, N.C., Farabaugh, S.M., Druker, B.B., 2002. Effects of Early Rearing Experience on

945 Adult Behavior and Nesting in Captive Hawaiian Crows (*Corvus hawaiiensis*). Zoo Biol. 21,

946 59-75.

947 Hediger, H., 1950. Wild Animals in Captivity. Butterworths, London.

948 Hesterman, H., Gregroy, N.G., Boardman, W.S.J., 2001. Deflighting procedures and their

949 welfare implications in captive birds. Anim. Welf. 10, 405-419.

950 Hetland, H., Choct, M., Svihus, B., 2004. Role of insoluble non-starch polysaccharides in

951 poultry nutrition. World's Poultry Sci. J. 60, 415-422.

952 Hocking, P.M., Maxwell, M.H., Mitchell, M.A., 1993. Welfare assessment of broiler breeder

953 and layer females subjected to food restriction and limited access to water during rearing.

954 Brit. Poultry Sci. 34, 443-458.

955 Huber-Eicher, B., Sebö, F., 2001. The prevalence of feather pecking and development in

956 commercial flocks of laying hens. Appl. Anim. Behav. Sci. 74, 223-231.

957 Hughes, B., 1973. The effect of implanted gonadal hormones on feather pecking and

958 cannibalism in pullets. Brit. Poultry Sci. 14, 341-348.

959 Hughes, B., 1985. Feather loss—how does it occur, Proceedings of the 2nd European

960 Poultry Welfare Symposium, Edinburgh, pp. 178-188.

961 Iglauer, F., Rasim, R., 1993. Treatment of psychogenic leather picking in psittacine birds

962 with a dopamine antagonist. J. Small Anim. Pract. 34, 564-566.

963 Ijichi, C.L., Collins, L.M., Elwood, R.W., 2013. Evidence for the role of personality in

964 stereotypy predisposition. Anim. Behav. 85, 1145-1151.

41

965   Jacobs, H., Smith, N., Smith, P., Smyth, L., Yew, P., Saibaba, P., Hau, J., 1995. Zebra finch

966   behaviour and effect of modest enrichment of standard cages. Anim. Welf. 4, 3-9.

967   Jaensch, S., 2000. Diagnosis of avian hepatic disease, Seminars in Avian and Exotic Pet

968   Medicine, Elsevier, pp. 126-135.

969   Jensen, P., Keeling, L., Schütz, K., Andersson, L., Mormède, P., Brändström, H., Forkman,

970   B., Kerje, S., Fredriksson, R., Ohlsson, C., Larsson, S., Mallmin, H., Kindmark, A., 2005.

971   Feather pecking in chickens is genetically related to behavioural and developmental traits.

972   Physiol. Behav. 86, 52-60.

973   Jones, T.A., Waitt, C.D., Dawkins, M.S., 2009. Water off a duck's back: showers and troughs

974   match ponds for improving duck welfare. Appl. Anim. Behav. Sci. 116, 52-57.

975   Keeling, L., Andersson, L., Schütz, K.E., Kerje, S., Fredriksson, R., Carlborg, Ö., Cornwallis,

976   C.K., Pizzari, T., Jensen, P., 2004. Chicken genomics: feather-pecking and victim

977   pigmentation. Nature 431, 645-646.

978   Keiper, R.R., 1969. Causal factors of stereotypies in caged birds. Anim. Behav. 17, 114-119.

979   Keiper, R.R., 1970. Studies of stereotypy function in the canary (*Serinus canarius*). Anim.

980   Behav. 18, 353-357.

981   Kjaer, J., Bessei, W., 2013. The interrelationships of nutrition and feather pecking in the

982   domestic fowl. Arch Geflügelk 77, 1-9.

983   Kjaer, J., Sørensen, P., 1997. Feather pecking behaviour in White Leghorns, a genetic

984   study. Brit. Poultry Sci. 38, 333-341.

985   Kjaer, J.B., 2009. Feather Pecking in Domestic Fowl is Genetically Related to Locomotor

986   Activity Levels: Implications for a Hyperactivity Disorder Model of Feather Pecking. Behav.

987   Genet. 39, 564-570.

42

988   Kjaer, J.B., Hjarvard, B.M., Jensen, K.H., Hansen-Møller, J., Naesbye Larsen, O., 2004.

989   Effects of haloperidol, a dopamine D2 receptor antagonist, on feather pecking behaviour in

990   laying hens. Appl. Anim. Behav. Sci. 86, 77-91.

991   Kjaer, J.B., Sørensen, P., Su, G., 2001. Divergent selection on feather pecking behaviour in

992   laying hens (*Gallus gallus domesticus*). Appl. Anim. Behav. Sci. 71, 229-239.

993   Kjaer, J.B., Würbel, H., Schrader, L., 2015. Perseveration in a guessing task by laying hens

994   selected for high or low levels of feather pecking does not support classification of feather

995   pecking as a stereotypy. Appl. Anim. Behav. Sci. 168, 56-60.

996   Klopfer, P.H., Hailman, J.P., 1972. Function and Evolution of Behavior. Addison-Wesley,

997   United States.

998   Koolhaas, J., Korte, S., De Boer, S., van der Vegt, B., van Reenen, C., Hopster, H., de Jong,

999   I., Ruis, M., Blokhuis, H., 1999. Coping styles in animals: current status in behavior and

1000   stress-physiology. Neurosci. Biobehav. R. 23, 925-935.

1001   Kops, M.S., Kjaer, J.B., Güntürkün, O., Westphal, K.G.C., Korte-Bouws, G.A.H., Olivier, B.,

1002   Korte, S.M., Bolhuis, J.E., 2017. Brain monoamine levels and behaviour of young and adult

1003   chickens genetically selected on feather pecking. Behav. Brain Res. 327, 11-20.

1004   Koštál, L., Savory, C., 1995. Serotonergic mechanisms in control of stereotypies in fowls.

1005   Appl. Anim. Behav. Sci. 44, 267.

1006   Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschlage, A., Mason, G., 2016.

1007   Stereotypic route-tracing in captive Carnivora is predicted by species-typical home range

1008   sizes and hunting styles. Anim. Behav. 117, 197-209.

1009   Labouriau, R., Kjaer, J., Abreu, G., Hedegaard, J., Buitenhuis, A., 2009. Analysis of severe

1010   feather pecking behavior in a high feather pecking selection line. Poultry Sci. 88, 2052-2062.

43

1011　Lambton, S.L., Knowles, T.G., Yorke, C., Nicol, C.J., 2010. The risk factors affecting the

1012　development of gentle and severe feather pecking in loose housed laying hens. Appl. Anim.

1013　Behav. Sci. 123, 32-42.

1014　Lang, M., Krátký, J., Shaver, J.H., Jerotijević, D., Xygalatas, D., 2015. Effects of anxiety on

1015　spontaneous ritualized behavior. Curr. Biol. 25, 1892-1897.

1016　Langen, M., Kas, M.J.H., Staal, W.G., van Engeland, H., Durston, S., 2011. The

1017　neurobiology of repetitive behavior: Of mice…. Neurosci. Biobehav. R. 35, 345-355.

1018　Laurence, A., Houdelier, C., Calandreau, L., Arnould, C., Favreau-Peigné, A., Leterrier, C.,

1019　Boissy, A., Lumineau, S., 2015. Environmental enrichment reduces behavioural alterations

1020　induced by chronic stress in Japanese quail. Animal 9, 331-338.

1021　Leipoldt, A.L., 1992. Gedrag van pekingeenden met variatie in drinkwatersysteem en

1022　bodembedekking. Praktijkonderzoek voor de Pluimveehouderij, PP-uitgave no. 03.

1023　Leitner, S., Catchpole, C.K., 2007. Song and brain development in canaries raised under

1024　different conditions of acoustic and social isolation over two years. Dev. Neurobiol. 67, 1478-

1025　1487.

1026　Lewis, M.H., Presti, M.F., Lewis, J.B., Turner, C.A., 2006. The Neurobiology of Stereotypy I:

1027　Environmental Complexity, in: Mason, G., Rushen, J. (Eds.), Stereotypic Animal Behaviour:

1028　Fundamentals and Applications to Welfare, CABI Oxfordshire, UK, pp. 190-226.

1029　Lumeij, J.T., Hommers, C.J., 2008. Foraging 'enrichment' as treatment for pterotillomania.

1030　Appl. Anim. Behav. Sci. 111, 85-94.

1031　Machlis, L.E., 1980. Apomorphine: Effects on the timing and sequencing of pecking behavior

1032　in chicks. Pharmacol. Biochem. Be. 13, 331-336.

44

1033   Marston, L.C., Bennett, P.C., Coleman, G.J., 2004. What Happens to Shelter Dogs? An

1034   Analysis of Data for 1 Year From Three Australian Shelters. J. Appl. Anim. Welf. Sci. 7, 27-

1035   47

1036   Martrenchar, A., Huonnic, D., Cotte, J., 2001. Influence of environmental enrichment on

1037   injurious pecking and perching behaviour in young turkeys. Brit. Poultry Sci. 42, 161-170.

1038   Mason, G., 2006a. Box 7.1 Are Wild-Born Animals 'Protected' from Stereotypy When Placed

1039   in Captivity?, in: Mason, G., Rushen, J. (Eds.), Stereotypic Animal Behaviour. Fundamentals

1040   and Applications to Welfare, CABI, Oxfordshire, UK, p. 196.

1041   Mason, G., 2006b. Stereotypic Behaviour in Captive Animals: Fundamentals and

1042   Implications for Welfare and Beyond, in: Mason, G., Rushen, J. (Eds.), Stereotypic Animal

1043   Behaviour: Fundamentals and Applications to Welfare, CAB International, Wallingford, pp.

1044   325-367.

1045   Mason, G.J., 1991a. Stereotypies and suffering. Behav. Process. 25, 103-115.

1046   Mason, G.J., 1991b. Stereotypies: a critical review. Anim. Behav. 41, 1015-1037.

1047   Mason, G.J., 2010. Species differences in responses to captivity: stress, welfare and the

1048   comparative method. Trends Ecol. Evol. 25, 713-721.

1049   Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: is stereotypy a reliable animal

1050   welfare indicator? Anim. Welf. 13, 57-69.

1051   Mayr, E., 1961. Cause and effect in biology. Science 134, 1501-1506.

1052   McAdie, T.M., Keeling, L., 2000. Effect of manipulating feathers of laying hens on the

1053   incidence of feather pecking and cannibalism. Appl. Anim. Behav. Sci. 68, 215-229.

45

1054 McBride, S.D., Long, L., 2001. Management of horses showing stereotypic behaviour, owner

1055 perception and the implications for welfare. Vet. Rec. 148, 799-802.

1056 McDonald Kinkaid, H.Y., 2015. Species-Level Determinants of Stereotypic Behaviour,

1057 Reproductive Success, and Lifespan in Captive Parrots (Psittaciformes), Animal and Poultry

1058 Science, University of Guelph, Canada.

1059 McKeegan, D.E., Savory, C., 1999. Feather eating in layer pullets and its possible role in the

1060 aetiology of feather pecking damage. Appl. Anim. Behav. Sci. 65, 73-85.

1061 Meehan, C.L., Garner, J.P., Mench, J.A., 2003a. Isosexual pair housing improves the

1062 welfare of young Amazon parrots. Appl. Anim. Behav. Sci. 81, 73-88.

1063 Meehan, C.L., Garner, J.P., Mench, J.A., 2004. Environmental enrichment and development

1064 of cage stereotypy in Orange-winged Amazon parrots (*Amazona amazonica*). Dev.

1065 Psychobiol. 44, 209-218.

1066 Meehan, C.L., Millam, J.R., Mench, J.A., 2003b. Foraging opportunity and increased

1067 physical complexity both prevent and reduce psychogenic feather picking by young Amazon

1068 parrots. Appl. Anim. Behav. Sci. 80, 71-85.

1069 Mellor, E., 2014. Can we use biological risk factors for stereotypic behaviour in parrots to

1070 predict husbandry risk factors? School of Biological Sciences, Plymouth University,

1071 Plymouth, UK.

1072 Mench, J.A., 2002. Broiler breeders: feed restriction and welfare. World's Poultry Sci.J. 58,

1073 23-29.

1074 Mertens, P.A., 1997. Pharmacological treatment of feather picking in pet birds. , In: Mills,

1075 D.S., Heath, S.E. (Eds.), Proceedings of the First International Conference on Veterinary

1076 Behavioral Medicine, UFAW, Potters Bar, UK., pp. 209-213.

46

1077   Meyer-Holzapfel, M., 1968. Abnormal behaviour in zoo animals, in: Fox, M.W. (Ed.),

1078   Abnormal Behaviour in Animals, Saunders, London, pp. 476-503.

1079   Miller, L.J., 2012. Visitor reaction to pacing behavior: influence on the perception of animal

1080   care and interest in supporting zoological institutions. Zoo Biol. 31, 242- 248.

1081   Moon-Fanelli, A.A., Dodman, N.H., O'Sullivan, R.L., 1999. Veterinary models of compulsive

1082   self-grooming: parallels with trichotillomania, in: Stein, D.J., Christenson, G.A., Hollander, E.

1083   (Eds.), Trichotillomania, American Psychiatric Press, Washington DC, USA, pp. 63-92.

1084   Morris, D., 1964. The response of animals to a restricted environment, Symposium of the

1085   Zoological Society., London, pp. 99-120.

1086   Morrissey, K.L.H., Widowski, T., Leeson, S., Sandilands, V., Arnone, A., Torres, J., 2014a.

1087   The effect of dietary alterations during rearing on growth, productivity, and behavior in broiler

1088   breeder females. Poultry Sci. 93, 285-295.

1089   Morrissey, K.L.H., Widowski, T., Leeson, S., Sandilands, V., Arnone, A., Torrey, S., 2014b.

1090   The effect of dietary alterations during rearing on feather condition in broiler breeder

1091   females. Poultry Sci. 93, 1636-1643.

1092   Müller, D.W., Lackey, L.B., Streich, W.J., Fickel, J., Hatt, J.M., Clauss, M., 2011. Mating

1093   system, feeding type and ex situ conservation effort determine life expectancy in captive

1094   ruminants. P. R. Soc. B 278, 2076-2080.

1095   Nettle, D., Penke, L., 2010. Personality: bridging the literatures from human psychology and

1096   behavioural ecology. Philos. T. Roy. Soc. B. 365, 4043-4050.

1097   Newberry, R.C., Keeling, L.J., Estevez, I., Bilčík, B., 2007. Behaviour when young as a

1098   predictor of severe feather pecking in adult laying hens: The redirected foraging hypothesis

1099   revisited. Appl. Anim. Behav. Sci. 107, 262-274.

1100   Nicol, C.J., 2015. Genetics and Domestication, The Behavioural Biology of Chickens, CABI,

1101   Oxfordshire, UK, pp. 1-14.

1102   Nicol, C.J., Lindberg, A.C., Phillips, A.J., Pope, S.J., Wilkins, L.J., Green, L.E., 2001.

1103   Influence of prior exposure to wood shavings on feather pecking, dustbathing and foraging in

1104   adult laying hens. Appl. Anim. Behav. Sci. 73, 141-155.

1105   Nielsen, B.L., Thodberg, K., Malmkvist, J., Steenfeldt, S., 2011. Proportion of insoluble fibre

1106   in the diet affects behaviour and hunger in broiler breeders growing at similar rates. Animal

1107   5, 1247-1258.

1108   Nordquist, R.E., Heerkens, J.L.T., Rodenburg, T.B., Boks, S., Ellen, E.D., van der Staay,

1109   F.J., 2011. Laying hens selected for low mortality: Behaviour in tests of fearfulness, anxiety

1110   and cognition. Appl. Anim. Behav. Sci. 131, 110-122.

1111   Nordquist, R.E., Zeinstra, E.C., Rodenburg, T.B., van der Staay, F.J., 2013. Effects of

1112   maternal care and selection for low mortality on tyrosine hydroxylase concentrations and cell

1113   soma size in hippocampus and nidopallium caudolaterale in adult laying hen. J. Anim. Sci.

1114   91, 137-146

1115   Norman, D.A., Shallice, T., 1986. Attention to action: willed and automatic control of

1116   behaviour., in: Davidson, R.J., Schwartz, G.E., Shapiro, D. (Eds.), Consciousness and self-

1117   regulation: advances in research and theory., Plenum Press, New York, pp. 1-18.

1118   Novak, M., 2003. Self-injurious behavior in rhesus monkeys: New insights into its etiology,

1119   physiology, and treatment. Am. J. Primatol. 59, 3–19.

1120   Ödberg, F., 1978. Abnormal behaviours: stereotypies., In: Garsi, E. (Ed.), Proceedings of the

1121   1st World Congress on Ethology Applied to Zootechnics, Industrias Graficas Espana,

1122   Madrid, pp. 475-480.

48

1123   Parmentier, H.K., Rodenburg, T.B., De Vries Reilingh, G., Beerda, B., Kemp, B., 2009. Does

1124   enhancement of specific immune responses predispose laying hens for feather pecking?

1125   Poult. Sci. 88, 536-542.

1126   Patzke, N., Ocklenburg, S., van der Staay, F.J., Güntürkün, O., Manns, M., 2009.

1127   Consequences of different housing conditions on brain morphology in laying hens. J. Chem.

1128   Neuroanat. 37, 141-148.

1129   Peng, S.J.-L., Chang, F.-C., Sheng-Ting, J.I., Fei, A.C.-Y., 2013. Welfare assessment of

1130   flight-restrained captive birds: effects of inhibition of locomotion. Thai J. Vet. Med. 43, 235.

1131   Perré, Y., Wauters, A.-M., Richard-Yris, M.-A., 2002. Influence of mothering on emotional

1132   and social reactivity of domestic pullets. Appl. Anim. Behav. Sci. 75, 133-146.

1133   Polanco, A., 2016. A Tinbergian review of self-injurious behaviors in laboratory rhesus

1134   macaques. Appl. Anim. Behav. Sci. 179, 1-10.

1135   Polverino, G., Manciocco, A., Vitale, A., Alleva, E., 2015. Stereotypic behaviours in

1136   *Melopsittacus undulatus*: Behavioural consequences of social and spatial limitations. Appl.

1137   Anim. Behav. Sci. 165, 143-155.

1138   Pomerantz, O., Meiri, S., Terkel, J., 2013. Socio-ecological factors correlate with levels of

1139   stereotypic behavior in zoo-housed primates. Behav. Process. 98, 85-91.

1140   Pötzsch, C.J., Lewis, K., Nicol, C.J., Green, L.E., 2001. A cross-sectional study of the

1141   prevalence of vent pecking in laying hens in alternative systems and its associations with

1142   feather pecking, management and disease. Appl. Anim. Behav. Sci. 74, 259-272.

1143   Quentin, M., Bouvarel, I., Picard, M., 2005. Effects of crude protein and lysine contents of

1144   the diet on growth and body composition of slow-growing commercial broilers from 42 to 77

1145   days of age. Anim. Res. 54, 113-122.

1146   Ramadan, S., von Borell, E., 2008. Role of loose feathers on the development of feather

1147   pecking in laying hens. Brit. Poultry Sci. 49, 250-256.

1148   Ramage, A., Bayles, K., Helm-Estabrooks, N., Cruz, R., 1999. Frequency of perseveration in

1149   normal subjects. Brain Lang. 66, 329-340.

1150   Riedstra B, Groothuis TGG. 2002. Early feather pecking as a form of social exploration: the

1151   effect of group stability on feather pecking and tonic immobility in domestic chicks. Appl.

1152   Anim. Behav. Sci. 77:127-138.

1153   Renema, R.A., Rustad, M.E., Robinson, F.E., 2007. Implications of changes to commercial

1154   broiler and broiler breeder body weight targets over the past 30 years. World's Poultry Sci. J.

1155   63, 457-472.

1156   Riber, A.B., Mench, J.A., 2008. Effects of feed-and water-based enrichment on activity and

1157   cannibalism in Muscovy ducklings. Appl. Anim. Behav. Sci. 114, 429-440.

1158   Riber, A.B., Wichman, A., Braastad, B.O., Forkman, B., 2007. Effects of broody hens on

1159   perch use, ground pecking, feather pecking and cannibalism in domestic fowl (*Gallus gallus*

1160   *domesticus*). Appl. Anim. Behav. Sci. 106, 39-51.

1161   Richards, M., Rosebrough, R., Coon, C., McMurtry, J., 2010. Feed intake regulation for the

1162   female broiler breeder: In theory and in practice. J. Appl. Poultry Res. 19, 182-193.

1163   Rodenburg, T., Bracke, M., Berk, J., Cooper, J., Faure, J., Guemene, D., Guy, G.,

1164   Harlander, A., Jones, T., Knierim, U., 2005. Welfare of ducks in European duck husbandry

1165   systems. World's Poultry Sci. J. 61, 633-646.

1166   Rodenburg, T., Buitenhuis, A., Ask, B., Uitdehaag, K., Koene, P., van der Poel, J.,

1167   Bovenhuis, H., 2003. Heritability of feather pecking and open-field response of laying hens at

1168   two different ages. Poultry Sci. 82, 861-867.

1169 Rodenburg, T., van Krimpen, M., de Jong, I., De Haas, E., Kops, M., Riedstra, B., Nordquist,

1170 R., Wagenaar, J., Bestman, M., Nicol, C., 2013. The prevention and control of feather

1171 pecking in laying hens: identifying the underlying principles. World's Poultry Sci. J. 69, 361-

1172 374.

1173 Sahakian, B.J., Robbins, T.W., Morgan, M.J., Iversen, S.D., 1975. The effects of

1174 psychomotor stimulants on stereotypy and locomotor activity in socially-deprived and control

1175 rats. Brain Res. 84, 195-205.

1176 Saint-Dizier, H., Leterrier, C., Lévy, F., Richard, S., 2008. Selection for tonic immobility

1177 duration does not affect the response to novelty in quail. Appl. Anim. Behav. Sci. 112, 297-

1178 306.

1179 Samson, J., 1996. Behavioral problems of farmed ostriches in Canada. Canadian Vet. J. 37,

1180 412-414.

1181 Sandilands, V., Tolkamp, B.J., Savory, C.J., Kyriazakis, I., 2006. Behaviour and welfare of

1182 broiler breeders fed qualitatively restricted diets during rearing: Are there viable alternatives

1183 to quantitative restriction? Appl. Anim. Behav. Sci. 96, 53-67.

1184 Savory, C.J., 1995. Feather pecking and cannibalism. World's Poultry Sci. J. 51, 215-219.

1185 Savory, C., 1998. Feather pecking damage in growing bantams is influenced by dietary

1186 tryptophan concentration but not dietary protein source. Brit. Poultry Sci. 39, 17-18.

1187 Savory, C., Mann, J., Macleod, M., 1999. Incidence of pecking damage in growing bantams

1188 in relation to food form, group size, stocking density, dietary tryptophan concentration and

1189 dietary protein source. Brit. Poultry Sci. 40, 579-584.

51

1190   Savory, C.J., Maros, K., Rutter, S.M., 1993. Assessment of Hunger in Growing Broiler

1191   Breeders in Relation to a Commercial Restricted Feeding Programme. Anim. Welf. 2, 131-

1192   152.

1193   Schmid, R., Doherr, M.G., Steiger, A., 2006. The influence of the breeding method on the

1194   behaviour of adult African grey parrots (*Psittacus erithacus*). Appl. Anim. Behav. Sci. 98,

1195   293-307.

1196   Sirén, M.J., 1963. A factor preventing cannibalism in cockerels. Life Sci. 2, 120-124.

1197   Snyder, N., Wieley, J., Kepler, C., 1987. The parrots of Luquillo: natural history and

1198   conservation of the Puerto Rican parrot. Western Foundation of Vertebrate Zoology. USA.

1199   Stokes, A.W., 1971. Parental and Courtship Feeding in Red Jungle Fowl. The Auk 88, 21-

1200   29.

1201   Svendsen, P.M., Hansen, B.K., Malmkvist, J., Hansen, S.W., Palme, R., Jeppesen, L.L.,

1202   2007. Selection against stereotypic behaviour may have contradictory consequences for the

1203   welfare of farm mink (*Mustela vison*). Appl. Anim. Behav. Sci. 107, 110-119.

1204   Tahamtani, F.M., Brantsæter, M., Nordgreen, J., Sandberg, E., Hansen, T.B., Nødtvedt, A.,

1205   Rodenburg, T.B., Moe, R.O., Janczak, A.M., 2016. Effects of litter provision during early

1206   rearing and environmental enrichment during the production phase on feather pecking and

1207   feather damage in laying hens. Poultry Sci.

1208   Tinbergen, N., 1963. On aims and methods of ethology. Zeitschrift für Tierpsychologie 20,

1209   410-433.

1210   Tolkamp, B.J., D'Eath, R.B., 2016. Hunger Associated with Restricted Feeding Systems, in:

1211   Phillips, C.J.C. (Ed.), Nutrition and the Welfare of Farm Animals Springer, Switzerland.

1212 Tweti, M., 2008. Of parrots and people: the sometimes funny, always fascinating, and often

1213 catastrophic collision of two intelligent species. Viking, New York.

1214 van Hierden, Y., 2003. Behavioural neurobiology of feather pecking, University of Groningen,

1215 The Netherlands.

1216 van Hierden, Y.M., de Boer, S.F., Koolhaas, J.M., Korte, S.M., 2004a. The control of feather

1217 pecking by serotonin. Behav. Neurosci. 118, 575.

1218 van Hierden, Y.M., Koolhaas, J.M., Korte, S.M., 2004b. Chronic increase of dietary l-

1219 tryptophan decreases gentle feather pecking behaviour. Appl. Anim. Behav. Sci. 89, 71-84.

1220 van Hierden, Y.M., Koolhaas, J.M., Košťál, L.u., Výboh, P., Sedlačková, M., Rajman, M.,

1221 Juráni, M., Mechiel Korte, S., 2005. Chicks from a high and low feather pecking line of laying

1222 hens differ in apomorphine sensitivity. Physiol. Behav. 84, 471-477.

1223 van Hierden, Y.M., Korte, S.M., Ruesink, E.W., van Reenen, C.G., Engel, B., Koolhaas,

1224 J.M., Blokhuis, H.J., 2002a. The development of feather pecking behaviour and targeting of

1225 pecking in chicks from a high and low feather pecking line of laying hens. Appl. Anim. Behav.

1226 Sci. 77, 183-196.

1227 van Hierden, Y.M., Korte, S.M., Ruesink, E.W., van Reenen, C.G., Engel, B., Korte-Bouws,

1228 G.A.H., Koolhaas, J.M., Blokhuis, H.J., 2002b. Adrenocortical reactivity and central serotonin

1229 and dopamine turnover in young chicks from a high and low feather-pecking line of laying

1230 hens. Physiol. Behav. 75, 653-659.

1231 van Hoek, C.S., King, C.E., 1997. Causation and influence of environmental enrichment on

1232 feather picking of the crimson-bellied conure (*Pyrrhura perlata perlata*). Zoo Biol. 16, 161-

1233 172.

53

1234   van Hoek, C.S., Ten Cate, C., 1998. Abnormal behaviour in cages birds kept as pets. J.

1235   Appl. Anim. Welf. Sci. 1, 51-64.

1236   van Horne, P., Achterbosch, T., 2008. Animal welfare in poultry production systems: impact

1237   of EU standards on world trade. World's Poultry Sci. J. 64, 40-52.

1238   van Krimpen, M., Kwakkel, R., André, G., van der Peet-Schwering, C., den Hartog, L.,

1239   Verstegen, M., 2007. Impact of nutritional factors on feather pecking behaviour of laying

1240   hens in non-cage housing systems, World Poultry Science Association, Proceedings of the

1241   16th European Symposium on Poultry Nutrition, Strasbourg, France, 26-30 August, 2007,

1242   World's Poultry Science Association (WPSA), pp. 415-422.

1243   van Krimpen, M., Kwakkel, R., van der Peet-Schwering, C., Den Hartog, L., Verstegen, M.,

1244   2009. Effects of nutrient dilution and nonstarch polysaccharide concentration in rearing and

1245   laying diets on eating behavior and feather damage of rearing and laying hens. Poultry Sci.

1246   88, 759-773.

1247   van Zeeland, Y.R., Schoemaker, N.J., 2014. Plumage disorders in psittacine birds-part 2:

1248   feather damaging behaviour. Eur. J. Companion Anim. Pract. 24, 24-36.

1249   van Zeeland, Y.R.A., Schoemaker, N.J., Ravesteijn, M.M., Mol, M., Lumeij, J.T., 2013a.

1250   Efficacy of foraging enrichments to increase foraging time in Grey parrots (*Psittacus*

1251   *erithacus erithacus*). Appl. Anim. Behav. Sci. 149, 87-102.

1252   van Zeeland, Y.R.A., Spruit, B.M., Rodenburg, T.B., Riedstra, B., van Hierden, Y.M.,

1253   Buitenhuis, B., Korte, S.M., Lumeij, J.T., 2009. Feather damaging behaviour in parrots: A

1254   review with consideration of comparative aspects. Appl. Anim. Behav. Sci. 121, 75-95.

1255   van Zeeland, Y.R.A., van der Aa, M.M.J.A., Vinke, C.M., Lumeij, J.T., Schoemaker, N.J.,

1256   2013b. Behavioural testing to determine differences between coping styles in Grey parrots

1257 (*Psittacus erithacus erithacus*) with and without feather damaging behaviour. Appl. Anim.

1258 Behav. Sci. 148, 218-231.

1259 Wang, S.-M., Kain, Z.N., White, P., 2008. Acupuncture analgesia: I. The scientific basis.

1260 Anesth. Analg. 106, 602-610.

1261 Wedel, A., 1999. Verhaltensstorungen, in: Wedel, A. (Ed.), Ziervogel–Erkrankungen,

1262 Haltung, Futterung, Parey Verlag im Blackwell Wissenschafts-Verlag,, Wien, pp. 283-286.

1263 Wickens, C.L., Heleski, C.R., 2010. Crib-biting behavior in horses: A review. Appl. Anim.

1264 Behav. Sci. 128, 1-9.

1265 Wiepkema, P.R., 1983. On the significance of ethological criteria for the assessment of

1266 animal welfare., In: Schmidt, D. (Ed.), Indicators Relevant to Farm Animal Welfare, Martinus

1267 Nijhoff, The Hague, pp. 71-79.

1268 Wilson, D.A., Clark, A.B., Coleman, K., Dearstyne, T., 1994. Shyness and boldness in

1269 humans and other animals. Trends Ecol. Evol. 9, 442-446.

1270 Wisely, J., Hare, D.J., Fernandez-Ford, L., 2002. A study of the topography and nature of

1271 self-injurious behaviour in people with learning disabilities. J. Intellect. Disabil. 6, 61-71.

1272 Würbel, H., Stauffacher, M., von Holst, D., 1996. Stereotypies in laboratory mice -

1273 quantitative and qualitative description of the ontogeny of 'wire-gnawing' and 'jumping' in ICR

1274 and ICR nu - mice. Ethology 102, 371-385.

1275

1276