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2017-09-23

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

10.1016/j.applanim.2017.09.011
Applied Animal Behaviour Science
Elsevier

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Abnormal repetitive behaviours in captive birds: a Tinbergian review

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

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

research on avian ARBs, to lead to a better understanding of ARBs in both well- and poorly-studied species, and to solutions/preventive measures to improve avian welfare.

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 of published literature is biased towards two species, domestic chickens, and European starlings, *Sturnus vulgaris*, and one order: Psittaciformes (parrots). Knowledge surrounding avian ARBs and, implicitly, welfare across this taxonomically diverse range of species remains currently limited to issues specific to these species. To address these issues, a holistic consideration of avian ARBs, permitting clear, broad predictions about susceptibility, amelioration and impact, across species and situations is now required.

The purpose of this review, therefore, is to provide a useful overview of ARBs across captive birds, taking advantage of the research effort on well-studied species, to give a starting point for future research. Tinbergen (1963) advocated that a comprehensive understanding of behaviour is only possible via a framework of posing 'Four Questions' (see also: Bateson and Laland, 2013). Thus, this review will follow his framework. Firstly, we address the proximate questions: development (how has the individual's ARB developed over time?), and causation (what are the internal and/or external mechanisms that trigger ARB?) (Mayr, 1961; Klopfer and Hailman, 1972). Next, we consider the ultimate questions: evolution (how can evolutionary history and genetics shape ARB?), and function (what is the value, if any, of ARB to the individual?) (Mayr, 1961; Klopfer and Hailman, 1972).

2. ARBs in birds

Table 1 summarises avian ARBs reported in the literature, loosely grouped based on similarities in outward form. Whether the superficial resemblance of some ARBs across different species is underpinned by shared causality is an important question that should be addressed in the future. Presently, however, there is not sufficient information to take an informed approach, an issue which further emphasises the need for this review. Therefore, our groupings are based on physical similarity and, importantly, do not imply similarity of development, causation, evolution or function (though we do not discount that future work might demonstrate such homologies).

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 recipent, 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)

and/or *Pacing:* moving forwards and back linearly along the ground, usually next to a cage wall or fence (Duncan and Wood-Gush, 1972; Degen et al., 1989; Glatz, 2000; Meehan et al., 2004)	European starlings, *Sturnus vulgaris* (Feenders and Bateson, 2012) Canaries, *Serinus canaria domestica* (Keiper, 1969) Green singing finches, *Serinus mozambicus* (Keiper, 1969) Gray singing finches, *Serinus leucopygius* (Keiper, 1969) Blue jays, *Cynanocitta cristata* (Keiper, 1969) 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).

Regarding feather-pecking (FP) in chickens, there are two forms commonly reported in the literature: severe and gentle (see Table 1). Herein, we indicate specific form if it has been reported, though this has not been always possible as authors do not always discriminate between the two (practically, this can be difficult for large flocks of birds). As will be seen, the two forms of FP have different welfare implications (*e.g.* McAdie and Keeling, 2000), and cases in which the two are pooled complicates the understanding of the basis for each. For this reason, we strongly encourage researchers during future studies to discriminate between the two forms of FP wherever possible.

TABLE 1 ABOUT HERE, PLEASE

2.1 Development

Development examines behavioural development over an individual's lifetime. Past experiences, life-stage (*i.e.* chick, juvenile, and adult), and hormonal and physiological profile all shape behaviour and susceptibility to ARB development.

2.1.1 Developmental trajectory of ARB

Several longitudinal studies have demonstrated the developmental trajectory of FP in laying hens (Huber-Eicher and Sebö, 2001; Lambton et al., 2010; Gilani et al., 2013). There is generally good agreement across studies that the prevalence and rates of the more damaging, severe FP increases as hens age, *e.g.* from 27% and 0.4 bouts per bird per hour during rear, to 65% and 1.9 bouts per bird per hour during lay (Gilani et al., 2013). The developmental trajectory of gentle FP is different, however, and either does not change or declines (*e.g.* Lambton et al., 2010; Gilani et al., 2013); supporting the argument that gentle and severe FP are different behaviours, with different welfare outcomes.

Although FP development is perhaps the best studied avian ARB, two longitudinal studies on orange-winged Amazon parrots, *Amazona amazonica* examined the development of several

ARBs in this species (Meehan et al., 2004). Two groups of birds, raised identically (captive-bred and parent-reared), were observed for 48 weeks from the age of 18-weeks. Whilst all were housed individually, ‘enriched’ parrots received foraging and physical enrichments, whereas ‘control’ parrots did not (Meehan et al., 2004). Control parrots developed oral and locomotor ARBs significantly sooner and more severely than enriched parrots, especially during the first 16 weeks (Meehan et al., 2004). While it is expected that ARBs increase during development if conditions remain unchanged, improving the environment, as demonstrated in this study, can slow their development. Hence, control parrots’ ARBs were significantly reduced when the enrichments were later provided (Meehan et al., 2004). Using the same experimental set up as above, this research group also reported a similar reduction in feather-damaging behaviour (FDB, see Table 1 for a description), again though enrichment provision (Meehan et al., 2003b).

2.1.2 Physiological development and ARBs

2.1.2.1 Sex

In some species, female birds are at increased risk of feather-directed behaviours, such as FP and FDB (Jensen et al., 2005; Garner et al., 2006; Mellor, 2014). For instance, 18% of females *versus* 7.9% of males feather-pecked in a red-jungle fowl, *Gallus gallus*, X white leghorn (a laying strain) population (Jensen et al., 2005), and female parrots are more FDB prone (McDonald Kinkaid et al., 2013; Mellor, 2014). Causal factors behind this female-bias are detailed in Section 2.2.1.3, but briefly the onset of lay (and associated rises in progesterone and oestrogen) is a key time in FP development (Hughes, 1973). The same is suggested to be true in FDB (Wedel, 1999), though experimental evidence for this is currently lacking.

2.1.2.2 Personality and stress response style

Personality, defined as consistent behavioural differences between individuals of the same species (Nettle and Penke, 2010), also relates to ARB. Orange-winged Amazon parrots with FDB showed more neuroticism-type personality traits, such as ‘fearfulness’ and ‘excitability’, whereas extraversion-type traits were negatively associated with locomotor ARBs (Cussen and Mench, 2015). The authors suggested personality influences an individual’s susceptibility to environmental stressors, here during enrichment deprivation, and thus ARB (Cussen and Mench, 2015).

Stress response style, or ‘coping’ style, a set of consistent behavioural and physiological responses to stress (Koolhaas et al., 1999), also affects susceptibility to ARB development. Two response styles are recognised, each with distinctive behaviours and physiological characteristics. ‘Proactive’ individuals have an active behavioural stress response, are ‘bold’ (*e.g.* will approach unfamiliar objects, *sensu*: Wilson et al., 1994), aggressive, impulsive, and are inclined towards routine formation (Koolhaas et al., 1999). ‘Reactive’ individuals have a passive behavioural stress response, are ‘shy’ (*e.g.* unlikely to approach unfamiliar objects, *sensu*: Wilson et al., 1994), are less aggressive, avoid risks, and behave flexibly (Koolhaas et al., 1999). Proactive individuals are characterised by low hypothalamus-pituitary-adrenal axis responsiveness and high sympathetic reactivity, whereas the opposite occurs in reactive individuals (Koolhaas et al., 1999). These differences in response style are suggested to predispose proactive individuals to ARB development (Koolhaas et al., 1999; Ijichi et al., 2013) with neurobiological differences being particularly influential (detailed in Section 2.2.1.2).

There are two avian examples of proactive susceptibility to ARB. Two strains of white leghorn chicken with contrasting propensity to FP also show differential response styles: high FPs tend to be proactive, and low FPs reactive (Blokhuis and Beutler, 1992; van Hierden et al., 2002a; van Hierden et al., 2002b). In African grey parrots, *Psittacus erithacus*, van Zeeland et al. (2013b) found some indication that parrots with FDB may have a proactive response style, but this was not consistent across different experiments. FDB status did not predict response style during a stressful event (manual restraint), but during novel object and open field tests parrots with FDB adopted a proactive style (van Zeeland et al., 2013b), *i.e.* they were bolder, and more likely to approach a novel object and explore during an open field test than birds without FDB.

2.1.3 Past experiences and ARBs

2.1.3.1 Rearing conditions

Rearing conditions experienced during early life influence ARB development. In laying hens, brooded (hen-reared) chicks are at less risk of developing FP when older (Perré et al., 2002) and are less likely to suffer FP and cannibalism-related mortality (Riber et al., 2007). Hand-reared African grey parrots (from 5 weeks old or less) are at increased risk of ARB as adults and are also more aggressive towards humans (Schmid et al., 2006). Contrastingly, though not directly comparable as all parent-reared birds were also wild-caught, hand-reared European starlings are less likely to perform somersaulting and other ARBs (Feenders and Bateson, 2012; but see: Coulon et al., 2014), are less fearful of humans (Feenders and Bateson, 2011), and do not show any indications of compromised cognitive function (Feenders and Bateson, 2013). As European starlings do not readily breed in captivity (Bateson and Feenders, 2010), whether this effect is one of hand-rearing or origin (wild *versus* captive) is unknown.

While not totally clear-cut in some cases, wild-caught birds may be more likely to develop ARBs than captive-bred. Wild-caught African grey parrots are more likely to display FDB than captive-bred individuals, regardless of captive-rearing technique (Schmid et al., 2006). Similarly, Keiper (1969) found his wild-caught blue jays, *Cyanocitta cristata*, performed more route-tracing but less spot-picking than captive-raised counterparts. This blue jay example suffers from the same confound as with the starlings, as captive-raised birds were all hand-reared, leaving it impossible to judge the most influential developmental factor.

Aside from parental contact, other appropriate conspecific social experiences can be important to young birds. Solitary- and hand-reared captive Hawaiian crows, *Corvus hawaiiensis,* show more ARB as adults compared with group-raised birds. They also display other behavioural problems such as impaired social skills, particularly towards mates (Harvey et al., 2002). Similarly, significant between-group behavioural differences were reported in young orange-winged Amazon parrots housed for a year in enriched cages, either individually or with a same-sex partner (Meehan et al., 2003a). None of the pair-housed parrots developed ARBs, yet 57% of the single-housed birds developed oral and/or locomotor ARBs, had a more restricted behavioural repertoire, were less active and more fearful: clearly demonstrating the importance of a cage-mate to the welfare of these birds (Meehan et al., 2003a). From these examples, it seems clear that parental/maternal and/or conspecific social contact whilst young is influential in avian behavioural development, including that of ARB.

2.1.3.2 Previous housing conditions

The experience of pecking or foraging opportunities during early life influences FP development in adult laying hens. For example, housing chicks on litter has been repeatedly shown to reduce FP or its effects at adulthood (Blokhuis and van der Haar, 1989; Bestman et al., 2009; Tahamtani et al., 2016), with even a short experience of litter protective against FP development to some degree (10 days: Nicol et al., 2001). Scattering grain in the litter (Blokhuis and van der Haar, 1992) and providing straw and objects to encourage pecking during rear can result in less FP when birds are older (notably, severe FP in turkeys, *Meleagris gallopavo*: Martrenchar et al., 2001). In these examples, lack of appropriate foraging and exploratory opportunities and/or other stimuli during rear may result in redirection of pecks towards flock-mates' feathers (*e.g.* Martrenchar et al., 2001; Bestman et al., 2009).

Experiencing and consuming loose feathers in the rearing environment may be a key risk factor for severe FP in laying hens. Hens moult three times during rear, so loose feathers are plentiful (Appleby et al., 1992). However, a relative shortage of loose feathers is then experienced during lay, resulting in pecking attention being redirected towards feathers still attached to flock-mates (McKeegan and Savory, 1999; Ramadan and von Borell, 2008). By regularly removing feathers from the rearing environment, Ramadan and von Borell (2008) demonstrated that hens who do not experience plentiful loose feathers during development are less likely to develop severe FP. Therefore, for laying hens 'learning' to peck at feathers when young seems a key developmental step for FP at later life.

2.2 Causation

The causation of behaviour or, as preferred by some, mechanism of control (Bateson and Laland, 2013) refers to internal and external stimuli triggering its performance. For internal triggers, we include the effects of neurotransmitters, hormones, brain function, and comorbidity with medical conditions. The current environment can be an external trigger for ARB, but separating out the effects of current and previous environments is problematic, though not a problem unique to ARB (Tinbergen, 1963; Bateson and Laland, 2013). To this end, ARB can be a 'scar' of welfare problems past and not necessarily indicative of the animal's current environment and welfare (*sensu*: Mason and Latham, 2004). To deal with this, we have limited ourselves in all but one example (Section 2.2.4.1) to discussing clear 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, 1993; Mertens, 1997). Rigorous experimental research is therefore now required to investigate relationships between DA, 5-HT and FDB.

2.2.1.2 Neurotransmitters and interaction with stress response style

As mentioned in Section 2.1.2.2, proactive animals are suggested to be predisposed to ARB development due to response style-specific differences in 5-HT and DA activity (Koolhaas et al., 1999; Ijichi et al., 2013) and sensitivity to manipulations of these systems (van Hierden, 2003). In line with this, proactive high FP laying chicks were more sensitive to the effects of a D_1 and D_2 receptor agonist (measured by increased hyperactive locomotion) (van Hierden et al., 2005). More support comes from a study that increased severe FP in high FP laying chicks by reducing 5-HT synthesis with a 5-HT_{1A} receptor agonist, yet observed no effect in low FP chicks (van Hierden et al., 2004a). Similarly, a significant reduction of gentle FP via dietary tryptophan supplementation was only found in high FP laying chicks (van Hierden et al., 2004b). The predicted relationship between response style (based on FP) and 5-HT and DA activity is not unequivocal, however. Variation is observed across life-stages (Buitenhuis et al., 2006; Kops, et al., 2017) and across different lines (*i.e.* whether purposefully selectively bred based on FP (Kops et al., 2017), or not (van Hierden et al., 2002b)), leaving the response style – ARB relationship a little unclear.

2.2.1.3 Hormones

The onset of lay in laying hens is a key time in FP; experimental manipulation of progesterone and oestrogen demonstrates the influence of these hormones (Hughes, 1973). 12-week old pullets received sex hormone releasing implants with un-implanted pullets used as controls (Hughes, 1973). By 18 weeks, progesterone and oestrogen together resulted in a large increase in FP, progesterone alone induced a lesser, but still significant, increase, and the usual dramatic onset of lay increase in FP was suppressed with testosterone administration from 18-24 weeks (Hughes, 1973). Given similarities in outward forms of FP and FDB and the female-bias (Garner et al., 2006; Mellor, 2014) it is reasonable to predict FDB may be similarly affected by hormonal control, a testable hypothesis.

2.2.1.4 Nutrient deficiencies and hunger

In laying hens, deficiencies in certain nutrients trigger exploratory behaviour, including pecking. These deficiencies are therefore implicated in FP (Kjaer and Bessei, 2013). This has been extensively reviewed elsewhere (*e.g.* van Krimpen et al., 2005; Kjaer and Bessei, 2013) so, aside from fibre, only a brief overview is provided here. Deficiencies in crude protein (*e.g.* Ambrosen and Petersen, 1997) and specific amino acids such as methionine (*e.g.* Harms and Russell, 1996; Elwinger et al., 2008), arginine (*e.g.* Sirén, 1963), and lysine (*e.g.* Quentin et al., 2005) have been linked to FP, which is quickly and effectively reduced when appropriate diets are fed (Kjaer and Bessei, 2013). Fibre positively affects gut motility, and increases satiety levels (Hetland et al., 2004; Rodenburg et al., 2013); inadequate provision of fibre is associated with severe FP (van Krimpen et al., 2009; Rodenburg et al., 2013). Ingested feathers act on the gut in a similar fashion to fibre, thus by consuming feathers birds may increase satiety (Harlander-Matauschek et al., 2006b). Interestingly, the morphology of severe FPs (though not gentle FPs) is similar to foraging pecks, indicating the likely motivational basis of severe FP (Dixon et al., 2008). FP followed by feather-eating, therefore, may allow the birds to meet a dietary and digestive need not provided by the diet (Rodenburg et al., 2013).

While FP is more commonly reported in laying strains, it is also reported in broiler breeders (de Jong and Guémené, 2011) and relates to hunger (Morrissey et al., 2014a). Strong artificial selection in broilers means birds can effectively reach slaughter weight through rapid weight gain; this weight gain and subsequent obesity damages long-term health and productivity of broiler breeders, especially females (Richards et al., 2010). To avoid this, broiler breeders are usually restricted to 25-50% of *ad libitum* intake (Savory et al., 1993; Renema et al., 2007), show signs of chronic hunger (Mench, 2002), and physiological indications of stress, indicating that such restriction is detrimental to welfare (*e.g.* Hocking et al., 1993; de Jong et al., 2002). Furthermore, feed-restriction and hunger are associated with FP and oral ARBs such as spot-pecking (Sandilands et al., 2006; D'Eath et al., 2009; Nielsen et al., 2011; Morrissey et al., 2014a; Morrissey et al., 2014b). To reduce hunger and improve welfare, studies have investigated the effects of 'alternative' diets. Alternative diets are typically qualitative-restrictive (high volume, low quality and energy) diets, prolonging feeding times, and/or contain appetite suppressants (*e.g.* calcium propionate) to reduce feeding motivation (*e.g.* Sandilands et al., 2006). These alternative diets are often, though not always, associated with positive behavioural indicators of welfare such as a reduction in FP and its effects, and more 'normal' foraging behaviour overall (reviewed by: Tolkamp and D'Eath, 2016). For example, Morrissey et al., 2014a; 2014b found feather condition was better in hens fed alternative compared with control diets. However, alternative diets are controversial due to uncertainties surrounding their welfare effects and whether underlying 'metabolic hunger' for nutrients and energy is actually satisfied (see: Tolkamp and D'Eath, 2016).

2.2.2 Medical conditions and ARBs

ARB is co-morbid with some avian medical conditions. *Escherichia coli* infections (Brunberg et al., 2016), intestinal worm related mortality rates, infectious bronchitis, and egg peritonitis are linked with FP in laying hens (Pötzsch et al., 2001). As damaged feathers can be visual cues for FP (Hughes, 1985; McAdie and Keeling, 2000), perhaps in some of these examples the altered appearance (including feathers) and behaviour of ill birds has a likewise effect. In parrots, FDB may coincide with endoparasite (*e.g. Giardia psittaci*, an intestinal protozon: Clyde and Patton, 1996; Doneley, 2009) and ectoparasite infections (*e.g.* quill mites, *Syringophilus* spp. Doneley, 2009), presumably irritating the skin and/or feathers, causing the bird to chew at or remove them. This is also the case with painful and/or irritating diseases (renal and liver disease: Jaensch, 2000; Burgos-Rodríguez, 2010; van Zeeland

and Schoemaker, 2014). In these instances, FDB may be localised to the painful area (*e.g.* in the synsacrum in parrots with renal disease: Burgos-Rodríguez, 2010), or generalised (van Zeeland and Schoemaker, 2014).

It should be noted that the examples given here are correlative and, in some cases, anecdotal only, *i.e.* causation cannot be inferred. There could be causal mechanism linking ill-health and ARB, or poor environmental conditions may be the underlying causal factor for both. Experimental manipulations may aide this distinction. By experimentally administering young laying hens with an immune challenge, Parmentier et al., (2009) showed a link between feather condition and immune response. Poorer plumage condition, and thus increased FP, was found in hens given a higher dose of human serum albumin, showing that an immune response alone is sufficient to trigger FP. While the precise causal link between immune response and FP was unclear, it neatly demonstrated the immune challenge itself was the influencing factor, providing clear direction for further work. In all these cases, however, if an ARB is just a symptom of disease, we would predict that successful disease treatment would also eliminate the ARB.

2.2.3 CNS dysfunction and ARBs

Altered brain function and physiology is associated with ARBs in various mammalian species, being best studied in humans (reviewed by: Garner, 2006), and is likewise suggested to be influential in some avian ARBs. ARB-related CNS dysfunction in birds can be assumed by analogy with known CNS dysfunction-induced behaviour problems in humans. Similarities between FDB and trichotillomania (plucking of hair) in humans for instance implies, as per trichotillomania, that CNS dysfunction underlies FDB (Moon-Fanelli et al., 1999; Garner et al., 2006). CNS dysfunction is also inferred experimentally, typically, by measuring perseveration. Perseveration – the inappropriate repetition of an ineffectual response – is used as a proxy for CNS dysfunction, because it may indicate problems with basal ganglia and other brain regions responsible for behaviour selection and control (Norman and Shallice, 1986; Garner, 2006). Perseveration positively correlated with ARB in orange-winged Amazon parrots (Garner et al., 2003b), blue tits, *Cyanistes caeruleus*, and marsh tits, *Poecile palustris*, (Garner et al., 2003a), and, although less definitively, in high FP laying hens (during an extinction learning task: Harlander-Matauschek et al., 2006a, but see: Kjaer et al., 2015).

Thus when perseveration is measured, overall, it does covary with ARB in birds, *i.e.* those performing the most ARB are the most perseverative. However, perseveration or perseverative tendencies are also linked to stress response style (*sensu*: Koolhaas et al., 1999; Coppens et al., 2010). The routine formation tendency of proactive individuals is due to non-pathological individual differences in brain structure (Coppens et al., 2010). Given that high FP laying hens tend to be proactive (Blokhuis and Beutler, 1992; van Hierden et al., 2002a; van Hierden et al., 2002b), if these hens are more perseverative than low FP hens, is this just a by-product of their response style? Or a sign of a dysfunctional CNS? More damningly, in humans at least, perseveration is also seen in ‘normal’ individuals without ARBs (*e.g.* Ramage et al., 1999). Therefore, it is unclear whether perseveration is a valid proxy of brain dysfunction in avian species.

2.2.4 Environmental triggers for ARB

Many environmental risk-factors have been identified for avian ARBs, but the causal connection between the trigger and the ARB is generally unknown.

Firstly, ARB may be triggered by discrete events. Pacing, for example, was induced in Japanese quail when novel objects were placed into the cage (Saint-Dizier et al., 2008). Likewise, and unexpectedly as prior to this only wild-caught birds had been reported to somersault, somersaulting was triggered in hand-reared starlings during an experiment investigating the potential enriching effects of videos of landscapes (Coulon et al., 2014).

Similarly, the removal of a preferred environment can trigger ARB. For instance, a move from large, group-housed aviaries into small single-occupancy cages quickly led to somersaulting in starlings and mild FDB in an African grey parrot (Feenders and Bateson, 2012; van Zeeland et al., 2013a). Negative contrast effects may play a role here too (*sensu:* Burman et al., 2008); for example, layer pullets switched from wood-shavings to slatted floors performed more FP than those housed on slatted floors throughout (Blokhuis and Arkes, 1984). It seems likely, given that ARBs were triggered so quickly in these examples, that the birds found these events aversive.

Frustrated motivation of species-specific behaviours can lead to ARB. Here, when the opportunity to perform the frustrated behaviour is provided, ARB should be reduced or even eliminated (Mason and Latham, 2004). For example, water for bathing is important to duck welfare (Jones et al., 2009), as illustrated by Riber and Mench (2008) who found FP was higher in farmed Muscovy ducklings, *Cairina moschata*, without water access than those with. Frustrated foraging motivation is often proposed to underlie oral ARBs and FDB (Meehan et al., 2003b; van Zeeland et al., 2009). Supporting this are reports of increased foraging times and reduced oral ARBs and FDB in canaries, *Serinus canaria domestica*, and African grey parrots, respectively, using foraging enrichments (Keiper, 1969; Lumeij and Hommers, 2008; van Zeeland et al., 2013a). More evidence comes from orange-winged Amazon parrots, as enrichment provision reduced the amount of ARB performed (unenriched birds performed more), but also changed the primary *form* of ARB (Meehan et al., 2004). Enriched birds performed predominantly locomotor ARBs, whereas the mix of locomotor and oral ARBs was more equal in unenriched birds (Meehan et al., 2004). Interestingly, in the latter group this changed when enrichment was later provided; locomotor ARBs became predominant in these birds too, implying the parrots' foraging 'needs' were almost completely satisfied by the added enrichments (Meehan et al., 2004). Note that while frustration would appear the most likely trigger in these examples, as ever, without careful experimentation we cannot state that other causal factors were not influential.

Finally, housing animals – including humans – in impoverished conditions can impair CNS development, causing dysfunction (Leipoldt, 1992; Lewis et al., 2006) and ARB (Hediger, 1950; Morris, 1964; Carlstead, 1998). Such conditions are regularly cited as causal in avian ARBs (Keiper, 1969; 1970; Jacobs et al., 1995; El-Lethey et al., 2000). Small and/or unenriched cages across numerous species are associated with increased ARBs, such as hopping in zebra finch, *Taeniopygia guttata* (Jacobs et al., 1995), oral ARBs in budgerigars, *Melopsittacus undulates* (Polverino et al., 2015), and route-tracing in canaries, (Keiper, 1969). Similarly, in young orange-winged Amazon parrots barren, unenriched cages reliably trigger FDB and other ARBs, which are successfully reduced with provision of physical and foraging enrichments (Meehan et al., 2003b; Meehan et al., 2004; Cussen and Mench, 2015). As the orange-winged Amazon parrots' ARBs were so easily reduced it seems unlikely that CNS dysfunction was an important causal factor; a hallmark of ARB driven by CNS dysfunction is that changing to more appropriate environmental conditions is unlikely to alter ARB (and may even make it worse) (reviewed by: Mason and Latham, 2004). Indeed, to the best of our knowledge just one study to date on laying hens has investigated the effects of different housing conditions on brain development. Patzke et al., (2009) reported only minor differences in key brain areas believed to be sensitive to environmental stimulation: hippocampal structures and the nidopallium caudolaterale. This somewhat unexpected result could indicate the adult avian brain may be less responsive to effects of environmental conditions than is that of young birds (*e.g.* Leitner and Catchpole, 2007; Patzke et al., 2009). However, as all the hens shared similar, possibly traumatic, pre-study rearing conditions, *i.e.* non-brooded, conditions known to affect behaviour (Edgar et al., 2016) and brain development (Nordquist et al., 2014) this early experience may have influenced early brain development across all hens and thus explain their results (Patzke et al., 2009). Therefore, this leaves plenty of scope to thoroughly investigate the effects of impoverished housing conditions on CNS development and ARB in birds across life-stages.

2.2.4.1 Flight restriction and ARB

Here, we detail one example where causation has not been adequately established, yet, we feel its implications for avian welfare warrants discussion. Two studies using survey data found various psittacine species to be at increased risk of FDB if unable to fly (pet African grey parrots (Schmid et al. 2006); preliminary results from 23 pet psittacine species (Mellor, 2014)). Causation cannot be inferred from these examples, but the results are intriguing as captive flight-adapted species often have their flight restricted or entirely prevented in captivity (van Hoek and Ten Cate, 1998; Hesterman et al., 2001). Indeed, partial wing-amputations did not diminish great-mynahs, *Acridotheres grandis*, preferences for large spaces with vertical height, implying the birds were still motivated to fly, even if not physically able (Peng et al., 2013). Preventing flight in captive birds may, therefore, represent a significant area of avian welfare concern.

2.3 Evolution

To understand the evolution of behaviour, Tinbergen (1963) advocated comparing the behaviour across a group related of species, and investigating the genetic control of species-specific behaviours. In this section, therefore, interspecific differences in ARB and heritability and genetics of ARB will be discussed.

2.3.1 Inter-specific differences in ARB

Phylogenetic comparative methods (PCMs) are useful in studying the evolution of behaviour, examining how it differs across a group of species and its co-evolution with other aspects of species biology and behaviour (Blumstein and Fernández-Juricic, 2010). In captive wild animal welfare studies, PCMs can be used to identify species-level risk-factors (*i.e.* species-typical traits) for poor captive welfare, including ARB (Clubb and Mason, 2003; Clubb and

Mason, 2007; Müller et al., 2011; Pomerantz et al., 2013; Kroshko et al., 2016; reviewed by: Mason, 2010).

Currently, McDonald Kinkaid (2015) has performed the only avian welfare PCM study, uncovering two risk-factors for poor welfare in parrots. Species with naturally effortful foraging modes, *e.g.* Ducorp's corella, *Cacatua ducorpsii*, were at increased risk of FDB (McDonald Kinkaid, 2015). The second risk-factor was relative brain volume; species with relatively large brains, *e.g.* red-shouldered macaws, *Diopsittaca nobilis*, were at increased risk of oral and locomotor ARBs (McDonald Kinkaid, 2015).

2.3.2. Intra-specific differences in ARB

2.3.2.1 Heritability

Selective breeding in laying hens demonstrates a possible heritable component to FP (*e.g.* Kjaer et al., 2001). FP heritability estimates (h^2) range from 0.07 – 0.54 (Cuthbertson, 1980; Bessei, 1984; Kjaer and Sørensen, 1997), and vary further between different breeds and lines (Faure et al., 2003). These estimates are somewhat confounded by the fact that social environment, *i.e.* flock mates, may also play a role in accurately estimating heritability for FP damage (Brinker et al., 2014). In addition, many studies aggregate data on *both* types of FP in their heritability estimates. This could be an important distinction to make, for Rodenburg et al. (2003) found while gentle FP was heritable in their study (h^2 at 5 weeks of age = 0.12; at 30 weeks = 0.15), severe FP was not. Therefore, assuming the two forms of FP really do represent two distinct behaviours, establishing the heritability of each and how this varies between life-stages is important.

Within a laboratory colony of orange-winged Amazon parrots, the h^2 estimate for FDB was 1.14 ± 0.27 (S.E.) (Garner et al., 2006). The estimate is greater than 1 as the small sample size featured full-siblings, limiting its generalisability; replication is now required with a larger, less related sample (van Zeeland et al., 2009). However, this does suggest, as with laying hens, it might be possible to select against FDB (Garner et al., 2006). Heritability of locomotor and oral ARBs in this study was low: $h^2 = -0.08 \pm 0.14$, though it is possible that the close relatedness, and thus little genetic variability, within their study group may explain this (Garner et al., 2006).

2.3.2.2 Genes

Molecular research has identified several genomic regions associated with FP. In adult laying hens possible quantitative trait loci (QTL), and clues of the likely location of genes for performing gentle and severe FP, were found on chromosome GGA2, and a potential one for receiving gentle FP on GGA5 (Buitenhuis et al., 2003a; 2003b). QTL locations for FP differed in 6-week old chicks though, performing gentle FP was located on GGA10, receiving gentle FP on GGA1, alongside further suggestive QTL on GGA2, 6, and 7 (Buitenhuis et al., 2003a). Biscarini et al. (2010) found good agreement with these QTL mapping studies, uncovering associations between giving and receiving FPs and single-nucleotide polymorphisms (SNPs) on many of the same chromosomes (see: Buitenhuis et al., 2003a; 2003b).

Specific gene-expression relates to FP. By comparing the genetic profiles of high and low FP laying hens, Flisikowski et al., (2009) uncovered two candidate genes associated with FP: DRD4 and DEAF1. These respectively encode for DA receptor D_4 and a 5-HT regulatory factor. Emerging evidence also suggests that some high FP laying hens show hyperactivity-type behaviour (Kjaer, 2009; Labouriau et al., 2009), perhaps underpinned by higher DA activity and thus a more active motor-system output overall (Kops et al., 2017). While the sample size was very small, Labouriau et al. (2009) reported differences in gene expression between the hyperactive high FPs (*N* = 4) and more ‘normal’ birds (*N* = 56), notably OPRD1 and OPRK, which relate to the opioid system (Labouriau et al., 2009). As well as these links to DA and 5-HT systems, FP is associated with genes directly and indirectly involved in absorption of nutrients from the intestine, glucose homeostasis, and the immune system

(Biscarini et al., 2010; Brunberg et al., 2011). Causal links between these genes and FP cannot be inferred from these studies, but they do further strengthen proposed relationships between FP and feeding motivation, and the DA and 5-HT systems.

Finally, research into the genetic profile of FP *victims* using white leghorn and red jungle fowl crosses, revealed a gene for feather pigmentation, PMEL17, predicted the severity of feather damage (Keeling et al., 2004). The white leghorn's dominant white allele (I) inhibits feather pigmentation, the wild-type recessive allele (i) results in some degree of feather pigmentation. Thus, recessive homozygotes (i/i) received the most FP damage, dominant homozygotes (I/I) the least, with heterozygotes (I/i) intermediate (Keeling et al., 2004). Wood-shavings in the litter were suggested to be more conspicuous on the feathers of pigmented birds, serving as a pecking stimulus (Keeling et al., 2004).

2.4 Function

In this section, the function of behaviour is considered. Generally speaking, behaviours increase the fitness of the individual, be it through increasing immediate survivorship, or reproductive output (*sensu*: Tinbergen, 1963). Where do ARBs fit into this? Common definitions of ARB emphasise its seemingly 'functionless' nature (Ödberg, 1978; Wiepkema, 1983); in some cases it is very difficult to see how ARBs serve to benefit the animal, *e.g.* self-damaging ARBs such as FDB leading to skin damage and infection (Meehan et al., 2003b; van Zeeland et al., 2009). However, combining evidence from better-studied taxa with a limited quantity of avian research, here we discuss potential functions of some specific cases of ARB, as well as considering cases where ARB may be functionless.

2.4.1 ARB and coping

ARB may calm an animal or facilitate coping with stressors. Firstly, ARB may reduce physiological stress (*e.g.* self-injurious biting in primates reduces heart rate: Novak, 2003), or alleviate signs of pain (*e.g.* crib-biting provides gastric irritation relief to horses: Wickens and Heleski, 2010), and is implied in FDB in parrots with renal disease (Burgos-Rodríguez, 2010). Additionally, ARB can be self-reinforcing ('DIY enrichments') and, as reported by humans, repetition itself is stress-relieving ('mantra effects') (Mason and Latham, 2004), allowing a regain of control and reduction in anxiety, especially after a stressful event (Eilam et al., 2011; Lang et al., 2015). When an ARB allows an animal to cope, in the Tinbergian sense "... the animal would be worse off if deprived of this attribute." (Tinbergen, 1963), ARB is thus associated with an improvement in welfare when the behaviour is performed (*sensu*: Mason and Latham, 2004).

Though 'coping' is widely suggested to underlie several avian ARBs (*e.g.* in conures, *Pyrrhura perlata perlata*: van Hoek and King, 1997), to the best of our knowledge, this has never been formally tested. We do, however, have two tentative potential avian coping examples. The first relates to FP, and eating, caused by low fibre diets in laying hens (van Krimpen et al., 2009), whereby birds could be coping by managing a dietary and digestive need not provided by the diet (see Section 2.2.1.4). Our second 'coping' example is FDB associated with a painful disease: *e.g.* in parrots with renal disease (see Section 2.2.2) (Burgos-Rodríguez, 2010). In humans, stimulating certain areas of the body reduces pain via endorphin release (termed acupuncture analgesia), in itself a reinforcing act (Wang et al., 2008). Self-harming humans and self-biting rhesus macaques target many of the same body areas (Wisely et al., 2002; Polanco, 2016). It is not implausible that FDB in this instance could be a do-it-yourself pain relief to alleviate disease-related pain.

Clearly, these hypotheses require testing, and the multi-factorial nature of FP and FDB means they may be coping mechanisms only under these very specific circumstances. We would predict, however, if ARB does allow the animal to cope, that indicators of improved welfare would be seen, such as decreased indications of hunger post-feather consumption by laying hens, and reductions in arousal, such as heart rate, during and immediately after a bout of FDB (based on: Novak, 2003), and that prevention of the ARB would negatively impact welfare (Mason and Latham, 2004).

2.4.2 ARB and CNS dysfunction

Finally, ARB may be indicative of an animal and its brain having been permanently altered by captivity. If perseveration is indicative of CNS dysfunction (but see Section 2.2.3) then in the perseverative orange-winged Amazon parrots, blue tits and marsh tits we may have evidence of CNS dysfunction (Garner et al., 2003a; Garner et al., 2003b). Logically we might also expect CNS changes to affect overall behaviour (*sensu*: Mason and Latham, 2004). Hawaiian crows may demonstrate such pervasive behavioural changes: as well as more ARB, adult crows raised in social isolation as chicks showed inappropriate play and social behaviour, especially towards mates, directly reducing reproductive output (Harvey et al., 2002). Associations between ARB and reduced reproductive success are reported in other species (American mink, *Neovison vison*: Díez-León et al., 2013). It therefore seems likely that signs of behavioural abnormality alongside ARB are indicative of an animal altered by captivity, with CNS pathology implicit in this. As such, for a bird with its behavioural repertoire shaped and affected by such conditions, it is most unlikely that ARB serves it any function.

3. Discussion and conclusions

This review has considered avian ARBs from Tinbergen's four interactive perspectives: development, causation, evolution, and function. Throughout, we have been limited to discussing a minority of representatives from this diverse taxonomic group. This does not mean absence of ARB evidence in other species equates to evidence of absence; more likely under- or non-reporting is the case. Given that thousands of avian species are held in captivity, and that the commonest captive bird species (domestic chicken) numbers in the billions, the extent of this could be far-reaching, leaving plentiful opportunities for future research. By reviewing different ARBs in the species discussed here, we hope this review provides a good starting point for researchers to go forward and investigate avian ARBs further, both in well-studied species and others. Below we summarise the four perspectives of avian ARBs, indicating current gaps in knowledge and directions for research.

In relation to development, female laying hens, jungle fowl, and parrots are at higher risk of FP (Jensen et al., 2005) and FDB (Garner et al., 2006; Mellor, 2014), with the onset of lay a crucial time in FP (Hughes, 1973). As evidenced in high FP laying hens (*e.g.* Blokhuis and Beutler, 1992) and, to a lesser extent, African grey parrots with FDB (van Zeeland et al., 2013b), birds with a proactive stress response style are more susceptible to ARB, though this now needs replication in other species. Studies on causation should be informed by knowledge of these developmental risk-factors for ARB, *e.g.* given the female-bias future studies might ask how sex hormones affect FDB. Additionally, the developmental trajectory of ARB is poorly described and understood in all but two species, and biased towards younger birds (*e.g.* Huber-Eicher and Sebö, 2001; Meehan et al., 2004). Therefore, this is a research area requiring attention, to unpick whether certain developmental windows are key to ARB at different life-stages, ARB ‘treatability’, and what this implies about the root cause(s) of ARB.

The rearing environment clearly influences ARB development. Providing opportunities to develop and perform highly motivated behaviours, such as foraging and environmental exploration, offers at least some protection against ARBs when older (FP: Blokhuis and van der Haar, 1989; Martrenchar et al., 2001; Nicol et al., 2001; Bestman et al., 2009; Tahamtani et al., 2016). Appropriate parental and social contact whilst young also shapes behavioural development, including ARB, in both precocial and altricial species (Harvey et al., 2002; Perré et al., 2002; Meehan et al., 2003a). However, early maternal separation and hand-rearing seem to be influential in ARB development in some (Schmid et al., 2006), but not all species (Feenders and Bateson, 2011; 2012; 2013). As an example, Riber et al., (2007) found that brooded layer chicks pecked the ground sooner and more often than non-brooded chicks. When older, brooded chicks also performed fewer severe FPs and suffered less cannibalism-related mortality than non-brooded (Riber et al., 2007).

Experience of wild conditions may predispose some species such as European starlings (Feenders and Bateson, 2012) and blue jays (Keiper, 1969) to ARB (with the caveat of rearing method confounds). Typically, the opposite is reported for wild-caught mammals, believed to be protected from ARB by their natural, complex upbringing (Mason, 2006a). Captivity can very quickly alter the behaviour of wild-caught birds. Butler et al. (2006) found time in captivity predicted behavioural responses of wild-caught chaffinches, *Fringilla coelebs*, during a foraging task, with chaffinches held the longest least likely to forage despite having lost the most weight. Furthermore, wild-caught parrots have a greater stress response to an acute stressor than parent-reared and captive-bred birds (Cabezas et al., 2013), and are those at highest risk of FDB (Schmid et al., 2006). This latter finding is especially important, as unlike the starlings and blue jays, the origin and ARB-risk relationship is not confounded by rearing technique, *i.e.* there are parent-reared captive-bred parrots for comparison. Perhaps therefore for some birds, in contrast to wild-caught mammals, the seemingly protective nature of a wild upbringing is outweighed by the acts of removal from the wild and introduction into captivity (with confinement being especially acute for an animal that usually inhabits a significant three-dimensional space). So much so, that behavioural indicators of compromised welfare, including ARB and other behavioural changes, quickly emerge.

Studies on internal causal triggers for ARB (principally in laying hens) implicate the roles of neurotransmitters, especially DA (*e.g.* Kjaer et al., 2004), sex hormones (Hughes, 1973), and dietary deficiencies (*e.g.* van Krimpen et al., 2007) on FP and other ARBs (*e.g.* Sandilands et al., 2006). Elevated DA activity is fairly clearly related to increased ARBs, but the relationship is less convincingly established between 5-HT and ARBs. Further examination of the variation in neurotransmitter–ARB relationships across life-stages (*e.g.* Kops et al., 2017) is another potentially fruitful area for future studies. The relationship between FP and sex hormones might be explained by changing nutritional needs of laying hens – potentially in female parrots with FDB too – due to the cost of egg production during lay. Energetic requirements increase at this time, and increased pecking may indicate increased feeding motivation, or hunger for nutrients which feathers may provide (Jensen et al., 2005). This could explain why FP is more commonly reported in laying strains of chicken, with their higher levels of egg production, than it is in broiler breeders.

CNS dysfunction is an important cause of ARB in other species (reviewed by: Garner, 2006), but it is not yet well-understood in birds. ARBs are reportedly extremely commonplace in some laboratory birds (up to 84.7% of active time in orange-winged Amazon parrots: Garner et al., 2006), with some evidence for CNS dysfunction (Garner et al., 2003b). Since laboratory-held birds are commonly used in behavioural research (Bateson and Feenders, 2010), a prevalence of CNS dysfunction and ARB would undermine the scientific validity of these models of 'normal' function, a matter of significant scientific concern (Garner et al., 2003b).

The environment can trigger ARB, though it is unclear *how* ARB is caused in most cases. Discrete, potentially aversive events such as moving cage (*e.g.* Feenders and Bateson, 2012) or removal of a preferred environment (*e.g.* Blokhuis and Arkes, 1984) can almost immediately trigger ARB, as can long-term housing in impoverished conditions (*e.g.* Meehan et al., 2004), and frustration of highly motivated behaviours (*e.g.* Riber and Mench, 2008). In order to efficiently address ARB, it is essential to first know how environmental conditions have caused the ARB. For instance, we might unnecessarily dismiss an environmental change or enrichment's ability to improve welfare in birds in which irreversible CNS dysfunction has already developed (reviewed by: Mason and Latham, 2004). Establishing causation is therefore fundamental in effectively improving welfare.

Species' evolutionary history can result in mismatches between how the species has evolved to behave and how the captive environment permits individuals to behave, resulting in ARB. Broiler chickens have been artificially selected for rapid weight gain driven by high feeding motivation, indeed, if permitted they eat far beyond what they require for energetic homeostasis (Richards et al., 2010). Broiler breeders are feed-restricted for health reasons (Richards et al., 2010), but with their high feeding motivation show signs of chronic hunger (Mench, 2002), triggering ARBs (*e.g.* FP: Morrissey et al., 2014a; oral ARBs: Sandilands et al. 2006; Nielsen et al., 2011). Likewise, wild parrots invest heavily in feeding and foraging (Snyder et al., 1987) and their captive counterparts are likely to be similarly motivated. It is perhaps unsurprising that naturally effortful foraging modes emerged as a risk-factor for FDB in parrots (McDonald Kinkaid, 2015), making it clear that for some, foraging behavioural needs are hard to facilitate in captivity. Thus, these evolutionary history mismatches, be it through natural or artificial selection, are influential in ARB and if understood can inform how best to improve welfare. To illustrate, tailoring enrichments to facilitate species-specific foraging modes that are known risk-factors for FDB may help protect against FDB development.

Flight, in species capable of flight, is one of the most constrained natural behaviours in captive birds, with restricted flight associated with ARB, as detailed in Section 2.2.4.1 (*e.g.* Schmid et al., 2006; Mellor, 2014). Whether negative welfare effects of flight restriction have exact parallels with spatial restrictions in mammals, or if there is something special about flight *per se* which when restricted in captivity compromises welfare, is unclear. To better understand this, future studies could make good use of PCMs to ask whether heavily flight-dependent species are at increased risk of poor captive welfare compared with those that fly less or not at all.

There is evidence for heritability in FP in laying hens and, perhaps, FDB in parrots (*e.g.* Kjaer et al., 2001; Garner et al., 2006). Based on this, it may seem logical to selectively breed against ARB, however, this may be costly. To start, other traits could be inadvertently selected for when selecting against ARB (for example, FP may have been accidently selected for whilst breeding for improved egg-production: Nicol, 2015). In divergent lines of mink based on ARB, the low ARB line were more fearful (Hansen and Jeppesen, 2006; Svendsen et al., 2007). Here, selection against ARB may have resulted in selection for apathy, another indication of poor welfare in itself (Fureix and Meagher, 2015). Therefore, purposefully selecting against ARB based on ARB alone is unwise. Early molecular work on genes associated with FP (*e.g.* Flisikowski et al., 2009; Biscarini et al., 2010; Brunberg et al., 2011), should now be developed further. Ideally future studies should examine other species (*e.g.* FDB and parrots) and incorporate evidence from causation studies, *e.g*. examining relationships between ARB and DA and 5-HT expression.

Lastly, we proposed two cautious suggestions of where ARBs may provide function to a bird by facilitating coping: FP and subsequent feather-eating in laying hens (*e.g.* van Krimpen et al., 2009), and FDB performance associated with disease-related pain (Burgos-Rodríguez, 2010). However, there is also some evidence of instances where ARB may result from a dysfunctional CNS (Garner et al., 2003a; Garner et al., 2003b), and is therefore unlikely to be functional. As implicit in this aetiology of ARB are negative welfare effects of impoverished living conditions (*e.g.* Hediger, 1950), we need to better understand how a bird's environment affects CNS development.

Many, if not all, of the avian ARBs described here are multi-factorial behaviours with complex aetiologies. Any approach taken to effectively understand and address them, therefore, needs to reflect this. For example, consider FP in laying hens. In severe FP *development*, the behaviour becomes more prevalent and frequent with age, particularly around the onset of lay, with proactive individuals especially predisposed to FP. Chicks' rearing conditions, such as 'learning' to eat loose feathers, also affect severe FP propensity in later life. In terms of *causation*, manipulations of neurotransmitters and sex hormones demonstrate the internal causal roles they have on FP, while dietary deficiencies and hunger are also important triggers. Considering the *evolutionary history* of FP, early artificial selection for increased egg-production may have inadvertently also selected for FP, and there are indications that FP may be heritable and under some degree of genetic influence. The *function* of severe FP, especially if birds consume the feathers they peck, may be to allow the hen to manage a nutritional need not provided by the diet. At present, severe FP is often managed commercially by routine beak-trimming (though it is banned or strictly controlled in some countries: van Horne and Achterbosch, 2008). However, beak-trimming is painful and addresses only the immediate outcome of the behaviour. The alternative approach, as evidenced in the review, is a comprehensive and multi-faceted study of the ARB. For instance: how does a rearing and adult environment with plentiful foraging opportunities interact with chicks being brooded to mitigate severe FP development? Can we select for personality or production traits, such as low mortality rate (see: Nordquist et al., 2011), that interact with these improved conditions in order to reduce FP? It is surely more effective and ethical to comprehensively consider ARB from every perspective, to understand and resolve the problem coherently rather than just addressing the immediate outcome. One important caveat in our above example is our use of evidence from research on severe FP and overall FP (*i.e.* severe and gentle FP is pooled). Unfortunately FP form is not always specified in scientific papers, though they are very likely distinct behaviours with differing welfare outcomes. We would therefore strongly encourage researchers to discriminate between the two forms of FP wherever possible.

To conclude, a diverse range of ARBs are performed by birds. Thousands of avian species are held in different captive settings, as pets, in zoos, as research animals, and extensively in food production, so the scale of ARB and the associated poor welfare is potentially huge. Employing Tinbergen's approach in investigating ARB highlights extensive gaps in our current knowledge. Key areas now requiring attention are: how ARB develops and changes over the course of an individual's lifetime; precisely how the environment causes ARB; a comprehensive investigation on a wide range of taxa to better understand evolutionary factors; and, lastly, directed studies to determine whether or not specific ARBs provide function to the performer. Finally, Tinbergen’s approach emphasises the complex, multi-factorial nature of ARB and, importantly, indicates how best to address them.

Conflicts of interest

None.

Acknowledgements

An earlier version of this review formed part of EM’s MSc, during which she was kindly part-funded by a Universities Federation for Animal Welfare Small Project and Travel Award (grant number: 62-13/14). We wish to thank Andrea Polanco, Georgia Mason, and three anonymous reviewers for their helpful thoughts and suggestions on previous drafts of this paper, whose comments much improved it.

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