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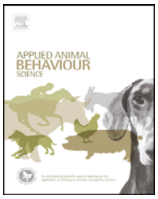

Review

Feather damaging behaviour in parrots: A review with consideration of comparative aspects

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ABSTRACT

Feather damaging behaviour (also referred to as feather picking or feather plucking) is a behavioural disorder that is frequently encountered in captive parrots. This disorder has many characteristics that are similar to trichotillomania, an impulse control disorder in humans. Unfortunately, to date much of the information regarding the aetiology and treatment in both syndromes is based on 'expert' opinion rather than on experimentally founded results. Comparative research in humans and parrots might therefore be mutually beneficial.

Feather damaging behaviour (FDB) may also share similarities with behavioural disorders present in other bird species. Feather pecking (FP) in poultry is of particular interest in this case. Because of the major impacts on welfare and economy, the disorder has been thoroughly investigated. It has been shown that genetic, socio-environmental and neurobiological factors all play a role in FP. Several theories have been postulated about the different motivational systems that affect the behaviour, of which (redirected) foraging appears to be the most generally accepted.

FDB may result from similar motivations and underlying mechanisms, but has also been regarded as a grooming disorder. Grooming or preening is behaviour that serves both physical and social purposes. In the presence of stressors, such as novelty, so-called displacement grooming may develop that can result in excessive grooming when chronic stress is experienced (*maladaptive behaviour*). Adrenocorticotropic hormone, opiate, dopaminergic and serotoninergic systems have been shown to influence the onset, development and maintenance of this behaviour.

Primary brain dysfunction (*malfunctional behaviour*) may also explain the occurrence of various abnormal behaviours. Differences in neurotransmitter levels and distribution have been found between high and low feather pecking lines of laying hens, and psychopharmacological interventions in humans and parrots suggest similar alterations. The exact pathways via which neurotransmitters influence the execution of these behaviours have not been identified. It is also not clear which brain areas are involved in

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this dysfunction, and why the behaviour sometimes persists despite intervention. For these purposes it is important to consider the current system-level insights on different types of abnormal repetitive behaviour, to which these disorders may be classified.

Contents

1. Introduction

In captivity, parrots are prone to develop a wide range of behavioural problems such as biting, screaming, feather picking, auto-mutilation, human-directed sexual behaviour and display of phobias or stereotypic behaviour (Davis, 1991; Meehan et al., 2004; Lightfoot and Nacewicz, 2006). In many cases, these problem behaviours may be interpreted as exaggeration or expansion of normal behaviour, resulting from inadequate environmental stimuli and/or early weaning and/or social isolation (Garner et al., 2003; Meehan et al., 2003b, 2004; Lightfoot and Nacewicz, 2006; Schmid et al., 2006). Among these behaviours, feather picking appears the most commonly recognized problem by the owners. As picking may only be a component of the behaviour, the term feather damaging behaviour (FDB) seems more appropriate (Orosz, 2006). Parrots with FDB either chew, bite and/or pluck their feathers with their beak (Harisson, 1986), which results in damage to the feathers and/or skin and may prevent normal regrowth of the feathers (Rosskopf and Woerpel, 1996). Grindlinger (1991) estimated that approximately 10 per cent of the captive parrot population suffers from FDB. As FDB implies a compromised welfare and is associated with medical problems, it has received growing attention over the last decade.

Research on FDB in parrots is currently in its infancy. The available knowledge is primarily based on clinical experience. There is great need for experimental studies, such as those conducted by Meehan et al. (2002, 2003a,b, 2004), to evaluate the importance of different aetiological factors. Detailed insight in the mechanisms underlying the behaviour will help in designing effective therapeutic strategies. Comparison to similar conditions in humans and other animal species may be valuable, as extrapolation of knowledge in these fields enhances comprehension of the disorder in parrots. Hair pulling, or trichotillomania (TTM), in humans and feather pecking (FP; cage-mate plucking) in laying hens, are particularly interesting in this respect, because of their apparent similarities in behaviour and targeting of similar stimuli, respectively.

The aim of the present paper is to summarize the current knowledge on FDB in parrots, TTM in humans and FP laying hens and investigate whether they share similar underlying mechanisms. In general, all three behaviours should be considered as undesirable, abnormal repetitive behaviour. In mammals, such as primates, cats and rodents, this repetitive behaviour can also be observed (Spruijt et al., 1992). These excessive grooming behaviours are potentially of additional interest, but are beyond the scope of this review. We will, however, mention them in light of normal grooming behaviour, its functions and mechanisms. It has been suggested that chronic stress from an inadequate environment may result in excessive (displacement) grooming and FDB, which can be considered as *maladaptive* behaviour. Behavioural disorders may also result from *malfunctional* behaviour, which is caused by a (primary) brain dysfunction or abnormal brain development. The current insights on the neurological systems involved in abnormal repetitive behaviour will therefore also be discussed. Subsequently, a comparative analysis will be made between the different disorders.

2. Feather damaging behaviour in parrots

2.1. Problem definition and phenomenology

Feather damaging behaviour in parrots, also referred to as feather picking or feather plucking, is a common problem in captive parrots (for a recent summary see Jenkins, 2001 and Seibert, 2006a,b). Its estimated prevalence is approximately 10 per cent (Grindlinger, 1991). FDB generally applies to all types of mutilation of the feathers by the beak and involves chewing, biting and plucking (Harisson, 1986). An important exclusion criterion for most other differential diagnoses is the presence of normal feather growth in areas inaccessible to the beak, particularly the head and crest (Galvin, 1983; Harisson, 1986; Westerhof and Lumeij, 1987). Feathers are mainly plucked on the easy accessible regions of the neck, chest, flank, inner thigh and wing web (Harisson, 1986; Van Hoek and King, 1997). Most authors state a preference for plucking feathers of the chest area (Rosenthal, 1993; Van Hoek and King, 1997; Nett and Tully, 2003). Additionally, the ventral wing area (Nett and Tully, 2003) or inner thighs (Rosenthal, 1993) are favoured regions. Contour and down feathers are generally identified as the main target. In some cases tail and flight feathers are affected. The latter instance usually involves chewing rather than plucking (Nett and Tully, 2003).

FDB is usually self-inflicted, but, when housed in groups, it can sometimes be directed to cage mates or nestlings. In these instances, the primary target area appears to be the head and face (Wedel, 1999; Fox and Millam, 2004; Lightfoot and Nacewicz, 2006). Interestingly, these are also the areas where allopreening is targeted (Van Hoek and King, 1997).

Usually FDB has merely aesthetic consequences for the parrot owner. However, in some cases medical problems arise, such as skin and tissue damage (predominantly in the pectoral region), hypothermia due to loss of insulation, infection and/or haemorrhage (Galvin, 1983; Rosenthal, 1993; Rosskopf and Woerpel, 1996).

2.2. Demographic characteristics of FDB

Although FDB may be noted in all psittacines, it is particularly common in Grey parrots (*Psittacus erithacus*), cockatoos (*Cacatua* spp.) and eclectus parrots (*Eclectus roratus*). It is less frequently seen in Amazon parrots (*Amazona* spp.), cockatiels (*Nymphicus hollandicus*) and budgerigars (*Melopsittacus undulatus*) (Chitty, 2003a,b; Seibert, 2006b). Grey parrots appear the most commonly presented species with FDB (Briscoe et al., 2001), although this may be biased due to the fact that this parrot is one of the most commonly held species (Dändliker, 1992). A higher incidence of self-inflicted soft tissue damage has been noted in cockatoo species, particularly Moluccan cockatoos (*Cacatua moluccensis*) and Umbrella or White cockatoos (*Cacatua alba*) (Rosenthal, 1993).

FDB often develops at the onset of sexual maturity, suggesting a role for hormonal control (Wedel, 1999). A female bias is reported for the orange-winged Amazon parrot (*Amazona amazonica*) (Garner et al., 2006). Often, cyclic or seasonal changes in the extent of FDB may occur, which have loosely been associated to dry air in the cold season or hormonal changes during the mating season. Birds may pluck continuously throughout their whole life, or pluck only for a single time during a short period (Lantermann, 1998).

2.3. Motivational backgrounds of FDB

Several theories exist concerning the motivational and aetiological backgrounds of FDB, such as habitual behaviour, comparable to nail-biting in humans (Johnson, 1987) or exaggeration of grooming behaviour due to changed time allocation in captivity (Harisson, 1986). Confinement may result in inability to engage in species-specific behaviours. Either a lack of social interaction ('redirected allogrooming') and/or deprivation of locomotor activities and/or foraging opportunities may be involved (Meehan et al., 2003a,b; Seibert, 2006b).

Based on their findings, Meehan et al. (2003a) postulated that 'redirected foraging' may be an underlying motivation for FDB, similar as suggested for FP in laying hens. Their results, however, were partially confounded with an increase in opportunities for additional exercise and physical complexity. The redirected foraging hypothesis has also been proposed and tested by Lumeij and Hommers (2008). This motivational explanation is particularly of interest since the time allotted to foraging differs greatly between parrots in captivity and in the wild state. Whereas birds in the wild spend up to 6 h on searching, selecting and manipulating food (Snyder et al., 1987), captive birds consume their food usually within 30–72 min (Oviatt and Millam, 1997). When birds are not able to engage their species-specific behaviour or are not provided appropriate target stimuli for these behaviours, FDB may develop (Jenkins, 2001). It is, however, not clear whether the lack of foraging may result in onset of FDB simply because of 'time consumption issues', or whether an underlying 'behavioural need' is involved (Meehan et al., 2003a; Lumeij and Hommers, 2008).

FDB may also be interpreted as a coping strategy for negative affective states (e.g. 'stress', 'loneliness', 'boredom') or housing in barren environments (Rosskopf and Woerpel, 1996; Levine, 1987). Findings in favour of the hypothesis that stress may be involved are described by Garner et al. (2006), who found distinctive room position effects on the occurrence of FDB. Parrots that were housed in proximity to the door showed significantly more FDB compared to individuals housed further away from the door, indicating presence of stressors as a causal factor. Influences of predictability of the environment, including sudden changes, have also been noted by others (e.g. Westerhof and Lumeij, 1987; Rosenthal, 1993). Initially the behaviour might occur as 'displacement grooming', which is often noted in situations with motivational ambivalence (Spruijt et al., 1992; see also Section 5.1). As preening has been associated with comfort or dearousal it may therefore be performed in times of stress (Delius, 1988).

The behaviour may eventually develop into abnormal repetitive behaviour (ARB). In these cases a changed neurochemistry and neuroanatomy may lead to persistence of the behaviour, even in absence of the original stressors or environmental deficits, similar to findings in other animals (Garner, 2006a; see also Section 6). Rearing conditions have been reported to influence behavioural development and occurrence of 'abnormal' behaviour, such as reaction to novel objects (Colette et al., 2000; Meehan and Mench, 2002; Meehan et al., 2003b; Fox and Millam, 2004; Luescher and Sheehan, 2005; Garner, 2006a). It has therefore been suggested that FDB may also represent *malfunctional* behaviour, resulting from abnormal brain development and altered neurochemistry.

Finally, exaggerated or prolonged reproductive behaviour has also been postulated as a possible motivation for FDB (Rosenthal, 1993). Birds naturally remove their feathers during the breeding season to create a brood patch (Oppenheimer, 1991). Especially when removal of the feathers occurs in the ventral area and is found to be seasonal (occurring during the breeding season), underlying hormonal changes and reproductive-associated behaviour may be involved (Rosskopf and Woerpel, 1996; Seibert, 2006b).

2.4. Aetiology of FDB

In general, two differential diagnoses should be taken into consideration for each behavioural problem, as designated by Mills (2003) and Garner (2005): (1) *maladaptive behaviour* resulting from attempts of the animal to behave normally in an abnormal or inadequate environment (either innate or learned); (2) *malfunctional behaviour* resulting from an abnormal psychology, brain development, or neurochemistry introduced by features of the captive environment. In parrots, a third group should also be considered, i.e. behaviour resulting from underlying *medical (physical) problems* (e.g. Seibert, 2006b).

FDB may be considered as maladaptive behaviour when preening (normal behaviour) increases in time, duration and/or intensity as a result of an attempt to respond to an inadequate environment. The suggestion that FDB indeed involves normal behaviour patterns is supported by the fact that: (1) it is often hard for the owner or observer to make a distinction between preening and FDB (e.g. Van Hoek and King, 1997), and (2) FDB often follows the same pattern as grooming (e.g. Lefebvre, 1982).

FDB in parrots is generally regarded as a multifactorial disease that may be influenced by a number of medical, genetic, neurobiologic and/or socio-environmental factors. Lantermann (1998) proposed that three main aspects of bird keeping can cause FDB: (1) cage size often restricts the bird's movements; (2) cage design and barrenness of the environment often do not provide sufficient behavioural opportunities to meet the parrots' high sensitivity, intelligence and behavioural needs; and (3) solitary housing, which fails to meet the high social needs of the bird.

2.4.1. Social and environmental factors

FDB is usually attributed to a variety of social causes that may include poor socialisation and absence of parents during the rearing period (subsequently resulting in failure to learn appropriate preening behaviours and routine). Several studies have focused on the importance of rearing methods (wild-caught, parent-raised, hand-reared) (Schmid, 2004; Luescher and Sheehan, 2005; Schmid et al., 2006). Maternal deprivation, with concurrent imprinting on humans in hand-reared parrots, may result in a failure to learn species-specific behaviour patterns (Wedel, 1999). Changes in brain development may also be a consequence of these deprivations in the early stages of life (Garner, 2006a).

However, there are no studies confirming this relationship in parrots, and no studies exist that relate abnormal brain development to FDB (see Section 2.4.2).

In captivity, pet birds are often kept isolated from conspecifics. Parrots are, however, highly social species, living in stable flocks under natural conditions (Nicol and Pope, 1993; May, 1996; Doneley, 2003; Seibert, 2006a) and may not deal well with a solitary lifestyle. Deprivation of a social or sexual partner (especially in reproductively active animals) may lead to separation anxiety, 'loneliness', 'boredom', sexual 'frustration' and/or 'attention-seeking' behaviour. These factors may all contribute to the onset of FDB (Davis, 1991; Gylstorff and Grimm, 1998; Wedel, 1999; Low, 2001), but no empirical studies have been performed to test these ideas.

Social interactions with either conspecifics or caregivers may be more or less important, dependent on rearing conditions (Schmid, 2004; Seibert, 2006b). Social bonds that are formed are strong, as birds often mate for life (Seibert, 2006a). For this reason it has been hypothesized that the sudden disappearance of a partner (avian or human) can lead to stress and associated FDB (Seibert, 2006b). Other sudden changes in the environment may also elicit FDB (Westerhof and Lumeij, 1987; Rosenthal, 1993). 'Unwanted' exposure to or contact with other animals of humans, may also be stressful for the bird and thus influence the onset of FDB (Seibert, 2006b). Additionally, inappropriate responses of the owner (e.g. punishing or attempting to distract the bird while it is feather picking) may reinforce the behaviour (Lightfoot and Nacewicz, 2006).

Absence of environmental complexity and enrichment, especially foraging opportunities, appears to influence the onset of FDB (Meehan et al., 2003a,b). 'Boredom' may also result from a lack of occupation or toys, or be the result of an improper cage size (Seibert, 2006b). Similar to other animals, environmental deprivation under rearing conditions may result in individuals that experience 'stress' and/or 'anxiety' under changed circumstances, and develop concurrent (neo)phobias and reduced motivation for exploration (Nicol and Pope, 1993; Meehan et al., 2003b; Luescher and Sheehan, 2005; Seibert, 2006b). Garner et al. (2006) found obvious room position effects on the occurrence of abnormal behaviour in Amazon parrots. In this study, neighbour effects were also examined. No correlation was found between feather picking levels of neighbour parrots. Thus, no evidence is present to indicate social transmission of FDB throughout a flock.

The abovementioned studies suggest that early-life history and a variety of socio-environmental factors (e.g. cage design, barrenness of the environment and solitary housing) may affect FDB. However, no research has been performed on the effect of cage size, as was proposed by Lantermann (1998). Additionally, it would be worthwhile to perform larger, experimental studies to study the effects of each of the abovementioned factors separately, particularly in parrot species prone to developing FDB.

2.4.2. Neurobiological factors

Little is currently known on brain dysfunction in FDB. However, it may be hypothesized that abnormal brain function is involved in FDB, especially in those cases that appear refractory to treatment with behavioural intervention and/or environmental changes. Neurotransmitter deficiencies have been proposed but not confirmed, although administration of the tricyclic antidepressants (TCA) clomipramine (Grindlinger and Ramsay, 1994) and doxepin (Johnson, 1987) in feather-plucking parrots has led to favourable results that support this hypothesis. These drugs, which are primarily used as antidepressants or anxiolytics, act as serotonin and norepinephrine reuptake inhibitors. They also display a function in α_1 receptor blockage and β receptor downregulation and postsynaptic antagonism of histamine H1-receptor and dopamine receptors (Gillman, 2007). Due to these various modes of action of TCA, it is hard to distinguish which action(s) is/are responsible for the effects.

Garner et al. (2003) found poor performance during a 'gambling task' in Amazon parrots displaying stereotypic behaviour, indicative of 'recurrent perseveration' (i.e. the inappropriate repetition of previous responses). Similar findings are encountered in humans with schizophrenia or autism (Frith and Done, 1983; Turner, 1997). 'Recurrent perseveration' is thought to be the result of disinhibition of responses within the contention scheduling system (CSS) that is located in the basal ganglia of the brain (Garner et al., 2003; Garner, 2006a; see also Section 6). Research on dysfunction of specific brain systems in feather picking parrots has not been performed.

2.4.3. Genetic factors

In Amazon parrots, a heritability estimate of 1.14 ± 0.27 was found for FDB, indicating that a genetic basis exists (Garner et al., 2006). This study, however, only involved analysis of full siblings and a small number of birds, explaining the heritability value of greater than 1. A larger data collection will be needed to get more reliable results. With regard to other parrot species, especially those that are prone to FDB, no information exists on possible underlying genetic factors. Quantitative trait loci (QTL) analysis could provide more insight in possible genetic markers that are involved in FDB (see also Section 4.4.3).

2.4.4. Medical and physical causes

Many medical causes underlying the development of FDB have been proposed, albeit without scientific documentation. Suggested causes include allergies (contact/inhalation/food), endoparasites, ectoparasites, skin irritation (e.g. by toxic substances, low humidity levels), skin desiccation, hypothyroidism, obesity, pain, reproductive disease, systemic illness (in particular liver and renal disease), hypocalcaemia, psittacine beak and feather disease (PBFD), proventricular dilatation syndrome, colic, giardiasis, psittacosis, airsacculitis, heavy metal toxicosis, bacterial or fungal folliculitis, genetic feather abnormalities, nutritional deficiencies (in particular vitamin A) and/or dietary imbalances, and neoplasia (Davis, 1991; Rosenthal, 1993; Juppien, 1996; Gylstorff and Grimm, 1998; Welle, 1999; Low, 2001; Seibert, 2006b). Iatrogenic causes, such as poor wing trimming, have also been described. It should be stressed that for many of the abovementioned factors a causative correlation has not been established, and may therefore merely be the result of coincidental findings.

When confronted with FDB in a parrot, 'underlying' medical problems (e.g. PBFD) should be ruled out by performing a complete physical examination, including blood chemistries, psittacine beak and feather disease testing and faecal examination (Lamberski, 1995; Welle, 1999; Forbes, 2002; Nett and Tully, 2003). Extensive history taking helps in identifying possible causes or triggering factors (Davis, 1991).

2.5. Triggering factors and cues

Little is known on the factors or cues that trigger a plucking bout. This may largely be explained by the difficulties that owners or caretakers have in distinguishing between FDB and grooming. Birds appear to have a preference for plucking already damaged feathers (Nett and Tully, 2003; Lightfoot and Nacewicz, 2006). To understand the underlying mechanism of FDB it is would be good to investigate under which situations FDB is initiated. One option would be to test whether experimentally damaged feathers or acute stressors trigger FDB. Assessing when exactly chronic stress, such as the absence of mates, increases the propensity to pluck, will be much more difficult.

2.6. Treatment modalities

Management of the condition often proves to be challenging, especially since it may be difficult to determine the antecedents and consequences that are associated with FDB. Furthermore, chronicity of the problem could have altered the disorder to become a habit. Many treatment modalities have been suggested in the veterinary literature, which include radical changes in housing and environment, with more toys and foraging activities (Kaleta, 2003; Meehan et al., 2003a; Lumeij and Hommers, 2008), pharmacological intervention (e.g. Seibert et al., 2004; Seibert, 2007), local application of foul tasting substances on the feathers and/or collars (Rosskopf and Woerpel, 1996; Davis, 1991). Thus far little evidence has been provided on the effectiveness of these treatment options.

2.6.1. Behavioural and environmental strategies

The combined application of appropriate foraging substrates and increased physical complexity can significantly decrease FDB (Meehan et al., 2003a). Psychological intervention for FDB typically involves environmental manipulation or behaviour therapy derived from operant theory (Davis, 1995; Seibert, 2006b). Promoting a more stimulating environment, by means of social contact, perches, chewing or puzzle toys, has been recommended (King, 1993; Bauck, 1998; Evans, 2001; Meehan and Mench, 2002; Meehan et al., 2003a, 2004). Environmental enrichment is important in the alteration of behaviour and in onset, prevention and treatment of FDB (Van Hoek and King, 1997; Meehan and Mench, 2002; Meehan et al., 2003a). In particular enrichment with foraging materials has been shown to improve feather condition (Lumeij and Hommers, 2008), as was proposed by Coulton et al. (1997) and Meehan et al. (2003a). Both 'competition for time' and 'fulfilment of behavioural needs' may explain these effects (Meehan et al., 2003a; Lumeij and Hommers, 2008).

Meehan et al. (2003b) also observed improved welfare and less abnormal behaviour in young Amazon parrots that were housed in isosexual pairs. However, as the social structure differs between Amazon parrots, cockatoos and Grey parrots (e.g. May, 1996; Doneley, 2003; Seibert, 2006a) this does not automatically imply similar effectiveness in all species.

2.6.2. Pharmacological intervention

Pharmacological intervention has been proposed (for a recent review see Seibert, 2007), of which the tricyclic antidepressant clomipramine is the best investigated (Grindlinger and Ramsay, 1994; Juarbe-Diaz, 2000; Seibert et al., 2004). A placebo-controlled trial in cockatoos showed reduced FDB after 3 and 6 weeks, but no changes in other behaviours, e.g. preening (Seibert et al., 2004). Other drug types have been used in the treatment of FDB. The selection of these drugs was based on their therapeutic success in compulsive behaviour in humans and other animals, which are associated with a decreased serotoninergic and an increased dopaminergic tone (Ridley, 1994; Aouizerate et al., 2005). Endorphins have also been implicated in compulsive behaviour, particularly self-injuring behaviour (Sandman and Hetrick, 1995). Drugs that influence the release or re-uptake of these neurotransmitters may subsequently affect compulsive behaviours. Examples of drugs claimed to be beneficial in the treatment of FDB in single cases are serotoninergic reuptake inhibitors (SRI's) such as paroxetine and fluoxetine (Mertens, 1997; Seibert, 2007), the dopamine antagonist haloperidol (Iglauer and Rasim, 1993; Lennox and VanderHeijden, 1993), and the opioid antagonist naltrexone (Turner, 1993). Anxiolytic drugs (e.g. diazepam; Galvin, 1983; Johnson, 1987) and hormones such as leuprolide acetate might also be beneficial in FDB in which specific causes (anxiety, hormonal changes) are suspected (Seibert et al., 2004). Due to lack of controlled studies concerning dosages, pharmacokinetics, toxicity and effectiveness, no recommendations can be made at this stage.

Based on the individual effects that have been attributed to these psychopharmaceuticals, it is proposed that multiple neurotransmitters may be involved in the neurobiology of FDB. However, it is important to realize that many of the drugs have a general effect on all behaviour by either blocking or enhancing their 'direct' (execution of behaviour) and/or 'indirect' (inhibition of behaviour) pathway (Garner, 2006a; Lewis et al., 2006), potentially masking the symptoms rather than treating them (Mills and Luescher, 2006).

3. Trichotillomania in humans

3.1. Problem definition and phenomenology

Trichotillomania, hair pulling or hair plucking in humans, was reported for the first time by the French dermatologist Hallopeau (1889). Until the 1990s TTM was considered relatively rare (Schacter, 1961; Mehregan, 1970; Muller, 1987), but since then an increasing number of cases have been reported, with a current estimated prevalence of 0.6–3.4% (Christenson et al., 1991a).

The disease often has a severe impact on psychosocial functioning (Diefenbach et al., 2005; Woods et al., 2006b). TTM has therefore been the subject of many studies (reviews by Diefenbach et al., 2000; Elliott and Fuqua, 2000; Hautmann et al., 2002; Woods et al., 2006c). Medical complications are uncommon, but may be life-threatening, e.g. in case of trichobezoars (hairballs in the stomach) (Muller, 1987).

In the fourth edition of the Diagnostic and Statistical Manual of Mental Disorders (DSM-IV, Anonymous, 1994) TTM is classified as an impulse control disorder, characterized by presence of 'impulses that cannot be controlled'. The diagnostic criteria for TTM–which distinguishes this psychopathologic disorder from other causes of chronic hair pulling–include: (1) recurrent hair pulling resulting in noticeable hair loss; (2) an increasing sense of tension immediately before pulling out the hair or when attempting to resist the behaviour; (3) pleasure, gratification, or relief when pulling out the hair; (4) no other mental disorders or medical conditions can be identified; and (5) the disturbance provokes clinically marked distress and/or impairment in occupational, social or other areas of functioning. Distinctive subtypes may exist, which may not fulfil all DSM IV criteria (Du Toit et al., 2001).

The body area most commonly involved is the scalp, but eyebrows, eye lashes, beard and moustache (in males), or, less commonly, hairs from the pubic or axillary area, trunk and extremities may also be target areas (Muller, 1987; Christenson et al., 1991b; Du Toit et al., 2001; Woods et al., 2006b). Hair pulling is usually directed at the individual itself, but it may also involve plucking of objects (e.g. dolls), pets, and even other people, especially in children (Tabatabai and Salarilak, 1981; Christenson and Mansueto, 1999).

TTM usually occurs daily, and may be carried out in one or more bouts, which can take up several hours (Soriano et al., 1996; Du Toit et al., 2001). The pulling is most often accomplished with the fingers, one-hair at a time, in a wavelike or centrifugal pattern (Koblenzer, 1987). Severe forms lead to baldness or fractured hairs (Koblenzer, 1987), or, in milder cases, to general thinning of the scalp hair (Christenson et al., 1991b). Periods of exacerbation or remission may occur. Especially in late-onset TTM the condition is often considered more severe and chronic (Swedo et al., 1992).

3.2. Demographic characteristics of TTM

TTM is more commonly reported in females. However, the greater willingness of females to seek medical care may bias these results and (partially) account for the differences (Azrin et al., 1980; Streichenwein and Thornby, 1995; Stanley et al., 1997; Du Toit et al., 2001; Woods et al., 2006a,b). Hormonal changes, in particular those related to the menstrual cycle, have been noted to influence the urge of hair pulling (Keuthen et al., 1997). No other clinically relevant differences between male and female hair pullers could be found (Christenson et al., 1994a).

The disease can already manifest itself between 11 and 13 years, in the phase of early childhood to adolescence (Greenberg and Sarner, 1965; Muller, 1987; Christenson et al., 1991b; Du Toit et al., 2001). Often, co-morbid problematic and compulsive behaviours, such as nail biting, may be present (Christenson et al., 1991b; King et al., 1995).

3.3. Motivational backgrounds of TTM

In people with TTM two distinguished types of hair pulling can be noted, i.e. 'automated' and 'focused' hair pulling (Christenson and Crow, 1996; Christenson and Mansueto, 1999). Focused hair pulling has been associated with negative emotions. It has therefore been proposed that hair pulling may serve as a coping strategy, both in low-arousal states (e.g. boredom) and high-arousal (tension, anxiety) states (Diefenbach et al., 2002, 2008; Penzel, 2003). In these instances, people may experience obvious tension and subsequent relief after the event. However, this kind of pulling only accounts for a small proportion of the behaviour (Stein et al., 1999).

Approximately 75% of the pulling occurs without the person being aware of it, which implies that it serves no emotional regulatory function (Christenson and Mansueto, 1999). It may therefore be considered *malfunctional* behaviour, which does not appear to serve any function. The disorder can be further classified as abnormal repetitive behaviour, and more specific as a compulsive/impulse control disorder. Individuals with TTM show a so-called 'stuck-in-set' perseveration, which indicates a disinhibition of cortical influence and change in corticostriatal pathways (Rettew et al., 1991; Keuthen et al., 1996; see also Section 6).

The direct consequences of hair pulling (e.g. tension relief) may positively or negatively reinforce this behaviour, and thus help to maintain TTM (Mansueto et al., 1991; Woods et al., 2006c).

3.4. Aetiology of TTM

Many factors have been suggested to influence the onset and course of TTM, but confirmation of a causal relationship is missing. This is mainly due to the small sample size and difficulty to design prospective experimental studies to test hypotheses derived from results of retrospective epidemiologic field surveys.

3.4.1. Social and environmental factors

Disturbed family and partner relationships and educational problems may play a role (Muller, 1987; Slagle and Martin, 1991; Lochner et al., 2002; Woods et al., 2006b). Traumatic events such as physical, mental and/or sexual abuse, emotional or physical neglect, parental separation and poor financial situation of the family may contribute to the onset of trichotillomania (Lochner et al., 2002; Wright and Holmes, 2003). Trichotillomania is also more common amongst people with a lower level of education and income (Muller, 1987; Slagle and Martin, 1991; Woods et al., 2006b).

3.4.2. Neurobiological factors

Neurochemical deficits have been proposed as well, but no experiments have been designed to confirm this. However, favourable outcomes with specific drugs led to the belief that this behaviour may be regulated and influenced by neurotransmitters (Swedo et al., 1989; Stein and Hollander, 1992; Christenson et al., 1994b). Particularly serotonin is believed to play a major role in mediating TTM, based on (1) its association with the execution of repetitive motor behaviours (Jacobs and Fornal, 1995); and (2) the significance of its dysfunction in OCD and other abnormal repetitive behaviours (Stein, 1996). The dopaminergic system and endogenous opiates are also of interest, because of the association with obsessive-compulsive symptoms, and its role in self-injurious behaviour, respectively (Stein et al., 1999).

A few studies confirm that differences exist in structure and function of the central nervous system between trichotillomanic patients and normal individuals, such as a reduction of the left putamen and left ventriculate volume, and decreased activity in the frontal and parietal regions and left caudate (Jenike et al., 1996; Stein et al., 2002). Particularly the corticostriatal circuits, which link the cortex and cerebellum, have been implicated (Stein et al., 1999).

3.4.3. Genetic factors

It has been suggested that a genetic basis for trichotillomania may exist (Lenane et al., 1992). A recently published twin-concordance study suggested a heritability estimate of 0.76 (Novak et al., 2009). However, thus far no specific set of genes has been identified in humans. A few studies did demonstrate that approximately 5–8% of first-degree relatives of TTM patients suffer from a similar condition, yet it remains debatable whether this is the result of genetic factors or environmental factors (Lenane et al., 1992; Schlosser et al., 1994).

3.4.4. Medical and physical causes

In rare cases, onset of TTM has been associated with medical problems, such as scalp or hair injuries or lice infestation (Christenson and Mansueto, 1999). It is, however, not possible to designate cause and effect in these cases.

3.5. Triggering factors and cues

Many different stimuli and situations may trigger an episode of hair pulling. Among these are physical features (e.g. texture, shape, colour) of the hair (Mansueto et al., 1991). It has been observed that the majority of bouts occurred in the evening during ‘relaxed’ or ‘sedentary’ situations, such as television watching and reading (Christenson et al., 1991b; Du Toit et al., 2001). Situations in which negative emotions are experienced are also cues that prompt or exacerbate hair pulling (Christenson et al., 1993).

Specific cognitions concerning the perceived appearance of the hair (e.g. lack of symmetry of the eyebrows), or negative beliefs concerning the individual’s appearance may attribute to the problem as well (Mansueto et al., 1991).

3.6. Treatment modalities

Prior to treatment of TTM, the individual’s (medical) history should be taken, in which the disorder, its effects and possible concomitant disorders are addressed. Among the treatment options that may be considered are (1) behaviour therapy (Azrin and Nunn, 1973; Azrin et al., 1980; Mansueto et al., 1999; Keijsers et al., 2006); (2) hypnosis (Rowen, 1981; Hynes, 1982; Hall and McGill, 1986); (3) insight-oriented psychotherapy, and (4) pharmacological therapy (Swedo et al., 1989). Physical restraint, such as wearing gloves, or treating the hair with petroleum or oil (Muller, 1987) have been used as well. These, however, serve merely as a means to prevent worsening of the situation in extreme cases, or help the patients to become aware of his/her actions.

Thus far, no large controlled trials have been performed to establish an effective treatment approach for trichotillomania. Instead, case reports, small case series and a few controlled and uncontrolled studies have presented a variety of treatment methods that merit further investigation. Other aspects that should be considered are the waxing and waning course of the disease and the subjectivity involved in (self-)assessment, which prove challenging to properly evaluate and compare treatment regimes.

3.6.1. Behavioural therapy and intervention

Behaviour therapies appear to be the most succesful strategy of intervention. Habit reversal training, in which patients are made aware of their habit and alternative coping responses are developed, seems very effective (Mansueto et al., 1999). Good short-term follow-up results have been recorded (Azrin and Nunn, 1973; Azrin et al., 1980; Rosenbaum and Allyon, 1981), but also a high percentage of relapses (up to 90% after 12 months) (Lerner et al., 1998; Keijsers et al., 2006). The occurrence of these relapses seems to be correlated to the severity of signs and level of depression, rather than age of onset or duration of the disorder. A complete absence of symptoms immediately after treatment proved to be the best predictor of long-term improvement (Lerner et al., 1998; Keijsers et al., 2006).

3.6.2. Pharmacological intervention

Many drugs have been employed that subsequently influence the levels of one or more neurotransmitters (serotonin, dopamine, endorphin) in the brain. The range of drugs that is used in TTM includes tricyclic antidepressants (amitriptyline, imipramine), serotoninergic reuptake inhibitors (fluoxetine, sertraline, trazodone), dopamine blocking neuroleptics (risperidone, olanzapine), opiate antagonists (naltrexone), anxiolytic drugs (e.g. buspirone, a serotonin 5-HT$_{1A}$ receptor partial agonist), and monoamine oxidase inhibitors (e.g. isocarboxazid), that act as antidepressants by increasing the availability of multiple neurotransmitters similar to tricyclic antidepressants (Snyder, 1980; Krishnan et al., 1984; Sachdeva and Sidhu, 1987; Parsons et al., 1989; Reid, 1992; Sunkureddi and Markovitz, 1993; Carrion, 1995; Stein et al., 1997; Epperson et al., 1999; Ravindran et al., 1999; Figgitt and McClellan, 2000; Stewart and Nejcek, 2003). However, results are usually limited to case reports and follow-up periods are usually short, whereas effects may be difficult to maintain long-term, especially in chronic cases (Swedo et al., 1993). Serotoninergic reuptake inhibitors have been studied more extensively, but placebo-controlled, double-blind crossover studies have failed to confirm their efficacy (Christenson et al., 1991c; Streichenwein and Thornby, 1995). The only drug found effective in controlled trials thus far seems clomipramine (Anafranil®; Swedo et al., 1989, 1993; Ninan et al., 2000). Clomipramine, however, is potentially toxic and is commonly linked to suicide attempts (Teicher et al., 1993). Thus, despite promising results, clomipramine is generally avoided in humans, especially in depressed individuals. Furthermore, a study by Bloch et al. (2007) has shown habit-reversal therapy to be superior to pharmacotherapeutic intervention with clomipramine. These results suggest that behaviour intervention should always be considered prior to attempting psychopharmacotherapy.

4. Feather pecking in laying hens

4.1. Problem definition and phenomenology

Feather pecking in laying hens is a behaviour that consists of the pecking at and pulling out of feathers of cage mates, and may exacerbate to cannibalism. Although in most cases FP is directed at other birds, self-plucking may also occur (Blokhuis et al., 1993). FP and cannibalism occur frequently in laying hens kept in commercial conditions (Savory, 1995). It may be encountered in a variety of different housing systems. Especially in large group housing systems FP is more difficult to control (Allen and Perry, 1975; Bessei et al., 1984; Appleby and Hughes, 1991; Buitenhuis, 2003). The reported prevalence can be as high as 40–77% of the flock (Huber-Eicher and Sebo, 2001), although implementation of several measures, in particular genetic selection, may lead to a significant decrease of FP within flocks (Rodenburg et al., 2004c; Ellen et al., 2008).

Due to the economical impact (loss of animals and reduced egg production) and welfare problems associated with FP, research groups from various countries (e.g. The Netherlands, Sweden, United Kingdom, Denmark) have investigated this behavioural disorder (e.g. Kjaer and Sørenson, 1997; Buitenhuis, 2003; Nicol et al., 2003; Riedstra, 2003; Rodenburg, 2003; Van Hierden, 2003; Rodenburg et al., 2004a; Jensen et al., 2005; Rodenburg and Koene, 2007).

When reviewing FP, it is important to realize that at least five different forms of bird-to-bird pecking can be distinguished (Savory, 1995): aggressive pecking (aimed at the head), gentle feather-pecking (causing little to no damage), severe feather-pecking (causing severe feather damage and pain), tissue pecking (aimed at denuded areas) and vent pecking. Only severe and gentle pecking are classified as FP. Gentle pecking can be further divided in three forms: (1) 'normal' gentle pecking in low frequencies, (2) stereotypic gentle pecking, characterized by high frequencies; and (3) gentle pecking at particles on the plumage, which may be mistaken for feather pecking behaviour (Savory, 1995). Preferred areas for FP include the neck, breast, back and vent (Wennrich, 1975; Harlander-Matauschek et al., 2007b). It has been reported that preference for particular areas varies from flock to flock (Harlander-Matauschek et al., 2007a), but no systematic experiments have been performed to confirm these differences.

4.2. Demographic characteristics of feather pecking

FP is considered a multifactorial disorder that is influenced by a variety of biological, social, environmental, and genetic factors. Gender and age can be considered as predisposing factors. Females have a stronger tendency to peck than males (Blokhuis and Arkes, 1984; Savory, 1995; Jensen et al., 2005), possibly resulting from hormonal influences (McKeegan and Savory, 2000). This may be one of the factors explaining the increase in FP around the onset-of-laying. The presence of hormonal influences is further supported by the findings that FP can be stimulated by administering a combination of oestrogen and progesterone, or blocked by giving testosterone (Hughes, 1973). FP can be observed as early as day 1 after hatching (Roden and Wechsler, 1998). Increases in the number of FP hens and frequency of pecks can be seen with age, with the highest frequency found around the onset of lay, at approximately 25 weeks of age (Hughes and Duncan, 1972; Jones et al., 1995; McKeegan and Savory, 2000; Huber-Eicher and Sebo, 2001). Early FP may affect the behaviour later on (Johnsen et al., 1998). A more recent study, however, has shown that there is no correlation between FP as a chick and FP at an older age (Buitenhuis et al., 2003a). Instead, a relationship between the frequency of ground-pecking and FP was recently suggested (Newberry et al., 2007).

4.3. Motivational backgrounds for feather pecking

It has been suggested that gentle FP may develop into stereotypic gentle FP and severe FP by either increased frequency or increased intensity (McAdie and Keeling, 2002; Riedstra, 2003). However, other studies failed to demonstrate gentle FP to be a good indicator for severe FP later on in life (Rodenburg et al., 2003; Newberry et al., 2007). Different motivational backgrounds are therefore likely to exist (Kjaer and Vestergaard, 1999).

Three different motivational backgrounds have been suggested for FP: (1) social exploration, which is particularly important at a young age to establish social bonds (Riedstra and Groothuis, 2002), (2) foraging (Blokhuis, 1986), and (3) dustbathing (Vestergaard et al., 1993; Johnsen and Vestergaard, 1996). Recent studies show that the motivational background may differ between the different forms of FP. Several studies are in support of the redirected ground-pecking hypothesis as the main cause for severe FP (Blokhuis, 1986; Huber-Eicher and Wechsler, 1998; Newberry et al., 2007). These studies also show that severe FP develops particularly in birds that are sensitive to changes in the environment. The social function of FP, on the other hand, is more obvious in gentle FP. Especially (non-stereotyped) gentle FP may be considered as a form of allopreening behaviour (Van Hierden et al., 2002a), that may serve as a means to reduce aggression and maintain social bonds (Wood-Gush and Rowland, 1973). The observations that more pecks are directed to unfamiliar than familiar chicks is also indicative of the social function of this behaviour (Zajonc et al., 1975; Riedstra and Groothuis, 2002).

4.4. Aetiology of feather pecking

4.4.1. Social and environmental factors

Social factors, including group size and density (Hughes and Duncan, 1972; Savory et al., 1999; Rodenburg and Koene, 2007), social rank (Hughes and Duncan, 1972; Vestergaard et al., 1993) and social learning–by imitation and stimulus enhancement–(Zeltner et al., 2000) may further influence onset, development and spread of FP among the flock.

Environmental parameters such as housing system (Green et al., 2000), feed composition (Van Krimpen et al., 2005; Van Krimpen, 2008), light (colour, intensity and frequency) (Kjaer and Vestergaard, 1999; Riedstra and Groothuis, 2004; Kristensen et al., 2007), presence of perches and floor substrate (Blokhuis, 1986; Harlander-Matauschek et al., 2006, 2007a; Whay et al., 2007) can also alter feather pecking frequency. It has been demonstrated that the behaviour is less likely to occur in 'enriched' environments (Hughes and Duncan, 1972; Blokhuis, 1986; Vestergaard et al., 1993; Huber-Eicher and Wechsler, 1998; Jones et al., 2000; McAdie and Keeling, 2002). Presence of 'enrichment' is particularly important at an early age (McAdie and Keeling, 2002; Chow and Hogan, 2005; Newberry et al., 2007), as this may influence stress and fear responses associated with environmental changes (El-lethey et al., 2000).

4.4.2. Neurobiological factors

A hen displaying a proactive coping style has an increased risk for developing compulsive disorders (Korte et al., 2005). Feather peckers indeed appear to show more a proactive rather than reactive coping strategy (Korte et al., 1997, 1999; Rodenburg et al., 2002, 2004b,c; Jensen et al., 2005). Each coping style has been associated with different plasma hormone and neurotransmitter levels. Corticosterone and serotonine levels were found to be significantly lower in FP individuals prior to and after manual restraint, whereas norepinephrine levels were significantly higher (Korte et al., 1997, 1999). In these laying hens, the occurrence of FP is influenced by high dopaminergic and low serotoninergic neurotransmission (Van Hierden, 2003; Van Hierden et al., 2002a,b, 2004a).

The link between FP and functional activity of the serotoninergic system is also evident from a study on genetic selection of FP. Whenever a decrease of FP was observed in a flock, a simultaneous decrease in fearfulness and increase in serotonin blood levels was found (Bolhuis et al., 2009).

4.4.3. Genetic factors

There is a large variation in the propensity to feather peck between different commercial lines. This suggests a strong genetic basis of feather pecking. In the undomesticated Red Jungle fowl feather pecking is also present (Vestergaard et al., 1993). Genetic predispositions and specific loci linked to FP have been found (Buitenhuis et al., 2003b; Keeling et al., 2004; Jensen et al., 2005). Heritability estimates for FP in a social context have been reported to range from 0.05 to 0.38 depending on the age (Kjaer and Sørenson, 1997; Rodenburg et al., 2003). Quantitative trait loci studies were performed that indicate that there may be a common gene or set of genes that affect both 'open-field behaviour' and feather pecking behaviour (Buitenhuis et al., 2003a,b).

Genetic selection within lines for decreasing and increasing FP based on individual selection has proven to be successful (Muir and Craig, 1998; Kjaer et al., 2001; Cheng et al., 2003; Cheng and Muir, 2004; Rodenburg et al., 2004c, 2008; Ellen et al., 2008).

4.5. Triggering factors and cues

It has been suggested that preen oil may affect the plumage taste and odour and therefore results in feather pecking of specific feathers and/or areas (Savory and Mann, 1999). The ease of feather removal and ease of access to certain parts of the body are also of influence (Bilcik and Keeling, 1999). McAdie and Keeling (2000) found that already damaged or ruffled feathers are an attractive stimulus for feather pecking. Furthermore, a colour specificity, with a higher preference for pecking at grey or black feathers rather than for white feathers, was recently demonstrated (Nätt et al., 2007).

Most studies on FP have focused on the feather peckers. Victims, however, are not selected at random (Keeling et al., 2004). Inactive chicks are more prone to become the target of both gentle and severe feather pecking (Riber and Forkman, 2007). Provision of shelter areas, as a means to avoid mixing of active and inactive individuals, has proven successful in these situations (Jensen et al., 2006). Between 9 and 12 weeks of age a change in targets occurs. During this period the targeted birds are mainly dustbathing individuals (Riber and Forkman, 2007). Two differing hypothesis exist to explain this phenomenon: (1) the actual dustbathing is a direct trigger for FP (Vestergaard et al., 1993), or (2) FP is induced by the higher proportion of litter in the plumage of a dustbathing individual (Savory et al., 1999). Other factors that might be linked to victims of pecking could be plumage characteristics (McAdie and Keeling, 2000), social position (Kjaer and Sørenson, 1997) or genetic predispositions (Kjaer and Sørenson, 1997; Riedstra and Groothuis, 2002; Buitenhuis et al., 2003a).

4.6. Treatment modalities

Beak-trimming has been an effective method to reduce feather damage and injuries due to FP (Blokhuis and Wiepkema, 1998). Dimming of lights or using red lights can also be used to calm birds down or avoid the detection of contrasts (between feathers and wounds). Both methods should, however, be considered more as damage control methods. Management changes aimed at reduction of risk factors seem more appropriate. Recently a potential new method for reducing FP has been suggested, whereby laying hens learn to avoid feathers soaked in quinine sulphate (Harlander-Matauschek et al., 2008).

4.6.1. Behavioural and environmental strategies

Environmental enrichment with foraging materials such as straw, branches, sand or wood shavings reduces FP (Huber-Eicher and Wechsler, 1998). Novel objects such as string devices, chains and ropes are also effective (Sherwin et al., 1999; Jones et al., 2000; Guy et al., 2001; McAdie et al., 2005). Other interventions that can affect FP are the physical form of the diet (i.e. mash, crumble or pellet), the distribution of particle size in a mash diet and provision of roughage supplements (e.g. cut green clover, maize-silage) (Van Krimpen et al., 2005). These measures will subsequently lead to a lengthening of the time spent on feed intake (Savory, 1974; El-lethey et al., 2000; Van Krimpen et al., 2005). Similar results can be found by (1) decreasing the energy content; and (2) increasing fibre content (Van Krimpen et al., 2005; Van Krimpen, 2008). Additionally, research has shown that several breeds and strains of chicken will choose food which requires work over freely available food (i.e. 'contrafreeloading') (Schütz and Jensen, 2001; Lindqvist et al., 2002, 2006), emphasizing the importance of foraging as a 'behavioural need'. These findings support the hypothesis of redirected foraging as the underlying motivation for FP.

4.6.2. Pharmacological intervention

Pharmacological intervention with haloperidol, a D2 receptor antagonist, can selectively reduce FP in chickens without presence of a sedative effect (Kjaer et al., 2004), suggesting that FP is influenced by the dopaminergic system. D2 receptors have been identified as regulators of the indirect pathways in the corticostriatal loops, which have been implicated in the onset of maintenance of abnormal repetitive behaviour, particularly stereotypies (McBride and Hemmings, 2005).

Dietary tryptophan suppletion, an essential amino acid from which serotonin is synthesized, can also reduce FP (Van Hierden et al., 2004b). Similar results were found with addition of other essential amino acids (methionine, cysteine, lysine and arginine) or minerals (zinc, sodium and magnesium) to the diet (Sirén, 1963; Elwinger et al., 2002; Van Krimpen et al., 2005).

5. Grooming behaviour and associated disorders—feather damaging behaviour as *maladaptive* behaviour?

5.1. Functions of grooming behaviour

Grooming consists of a variety of behaviours directed at the outer body surface and fulfils multiple functions in both mammals and birds. In the latter it is also referred to as 'preening'. First of all, grooming is essential for maintenance of skin, fur and/or feathers. Its performance may lead to (1) rearrangement of hairs/feathers, e.g. after bathing in water or dust; (2) removal of foreign objects, dirt, grease and/or parasites; (3) application of substances such as preen gland oil or saliva onto the body surface (e.g. for water proofing in waterfowl or regulation of body temperature in rodents); and (4) sensory stimulation of the skin (Delius, 1988; Spruijt et al., 1992).

Grooming may also serve a social function, especially when it is directed at the body of conspecifics (social grooming or allopreening) (Delius, 1988; Spruijt et al., 1992). This is particularly recognized in birds, in which preening is incorporated in the courtship rituals (McKinney, 1965), and primates (Goosen, 1987). Grooming behaviours may represent signals to indicate appeasement and help in establishing, maintaining, renewing and/or strengthening bonds between individuals. In rodents (and other mammals), the spread of chemical substances on the skin during self-grooming may also serve a social function (Wiepkema, 1979).

5.2. Grooming as a coping strategy?

Comfort behaviours, such as grooming, are generally associated with tension release after the animal has been in a state of high behavioural arousal (Holland, 1976; Delius, 1979). In situations in which two (conflicting) behavioural systems are activated or the course of a routine behaviour is blocked, so-called displacement grooming behaviour may be observed (Sevenster, 1961; Delius, 1979). According to disinhibition theory, 'low-priority' grooming behaviour will be performed immediately after activities such as social contact (including copulation) and exploration (especially of novel objects), and usually also precedes sleeping (Sevenster, 1961). Grooming may thus fill in time gaps left between 'high-priority' behaviours, as its performance is not critically coupled to a certain stimulus context, time or place. Furthermore, grooming behaviour may also be elicited directly after states of arousal because of disturbance of the skin surface, which subsequently increases the intensity of the provoking stimulus for skin care (Spruijt et al., 1992). Additionally, grooming is considered as a self-rewarding behaviour, related to release of endorphins (Van Ree et al., 2000). When stress is experienced, this behavioural system may subsequently be sensitized and run out of control (Cabib, 2006). These abovementioned theories may explain why grooming behaviour serves a function as coping strategy when (chronic) stress is involved. This may also apply to FDB in parrots, which may be considered as an adaptive behaviour of the animal to try and cope in an unsuitable environment.

5.3. Neurological and hormonal control of grooming behaviour

Grooming behaviour appears to be strongly controlled by internally programmed routines. Its neural and hormonal regulation has been most extensively researched in rats (Spruijt et al., 1992). Grooming behaviour may be controlled by peripheral sensory input or centrally coordinated programs. The importance of either system is highly dependent on the motivational context and sequential phase of grooming (Fentress, 1988). Stereotyped forms seem less dependent on peripheral stimuli, whereas short bouts of grooming usually occur in reaction to specific environmental stimuli (Lefebvre, 1982; Delius, 1988; Fentress, 1988; Sachs, 1988). Thus, both may serve a different function.

In particular the stereotyped form seems to be of interest in context of FDB. In all cases, a high perseverance of the behaviour can be noted. The behaviour may serve a compensatory function, in which internal reward systems are involved that compensate for the inability to perform other essential behavioural needs (e.g. dustbathing, foraging) (Spruijt et al., 2001). A variety of different neuropeptides act as regulators and modulators of grooming behaviour, e.g. ACTH (Ferrari, 1958; Gispen et al., 1976), endorphins (Spruijt et al., 1988), dopamine (Lindenblatt, 1986; Spruijt et al., 1986) and serotonin (Traber et al., 1988). These may also serve similar functions in the onset and maintenance of behavioural disorders such as FDB.

6. Current insights on neuropathophysiology of abnormal repetitive behaviour—feather damaging behaviour as *malfunctional* behaviour?

Besides the explanation that behavioural disorders have an adaptive function it should be considered that abnormal brain function may be involved. This dysfunction may be the result of a mixture of gene-environmental interactions affecting the structure and connectivity of the brain (Lewis et al., 2006).

Both in humans and animals different forms of abnormal repetitive behaviours are recognized, which may share similar underlying mechanisms (Mason, 1991). Within the wide range of ARB that are recognized, two major categories can be distinguished, i.e. stereotypies and compulsive/impulsive behaviours (Garner, 1999). In both instances, a disinhibition of behaviour or responses is present, which is mainly regulated via the ‘indirect pathway’ (that inhibits responses) rather than the ‘direct pathway’ (that activates responses) (Garner, 2006b).

Stereotypies and impulsive/compulsive behaviours are controlled by different systems (Turner, 1997); the contention scheduling system and the supervisory attentional system (SAS). The CSS is responsible for the selection and sequencing of behavioural responses on the basis of external stimuli (‘stimulus-response’). The SAS modulates the action of the CSS on the basis of internal context (‘cognitive’ control) (Norman and Shallice, 1986; Garner, 2006a). The performance of these two brain systems can be assessed with neuropsychological tests (Garner, 2006a).

Stereotypies are a group of disorders that are characterized by presence of ‘recurrent perseveration’, i.e. an inappropriate repetition of responses or complex motor programs. These tasks are primarily executed by the contention scheduling system, which is anatomically located within the basal ganglia (Garner, 2006a).

Impulse control disorders (ICD) and compulsive disorders (CD) are characterized by an inappropriate repetition of goals or abstract rules, with flexibility between the individual responses (stuck-in-set perseveration). Behaviours related to ‘stuck-in-set’ perseveration are ascribed to malfunctioning of the supervisory attentional system, which is located in the prefrontal cortex, and is related to ‘cognitive control’ (Garner, 2006a).

Identification of the type of perseveration therefore helps to categorize the behavioural disorder as either stereotypy or ICD/CD, and indicates which area of the brain is dysfunctional. Amazon parrots displaying stereotypic behaviours were found to exhibit ‘recurrent perseveration’ when performing a ‘gambling task’ (Garner et al., 2003). Similar studies may be designed to indicate which type of perseveration is present in birds with FDB. Considering that birds with FDB usually do not pluck repetitively according to a fixed pattern of motor actions, but rather target the same area or goal (Rosenthal, 1993; Nett and Tully, 2003), it may be hypothesized that this behavioural disorder most likely is an ICD/CD. Hence, these birds should display the ‘stuck-in-set perseveration’ that is characteristic for ICD. Research is warranted to test this hypothesis.

7. Discussion

Due to its complexity, in combination with a relative lack of scientific reports, FDB in parrots is one of the most challenging behavioural problems in veterinary medicine. Comparison to (seemingly) similar conditions such as TTM in humans, and FP in laying hens, is warranted to help gain insight in the disease and provide guidelines for future research. Table 1 summarizes the phenomenological characteristics, demographic features, aetiologic, motivational and triggering factors that may predispose to these three behavioural disorders, and addresses their current treatment modalities.

7.1. Comparison of FDB and TTM–feather damaging behaviour in parrots as a model for human TTM?

Already in the early 1990s, several researchers proposed FDB in parrots to be a potential animal model for TTM (Bordnick et al., 1994; Stein and Dodmann, 1994; Dodmann et al., 1997; Moon-Fanelli et al., 1999). Analogies were considered to exist with respect to behaviour, proposed aetiologies, evoking cues, response to behaviour therapy, and response to pharmacological therapies, such as serotonin reuptake inhibitors. These reports, however, presented little evidence, relying predominantly on anecdotes and ‘expert opinion’.

Since then, several systematic studies on FDB and other behavioural disorders have been published. These studies (e.g. Meehan and Mench, 2002; Meehan et al., 2003a, 2004; Fox and Millam, 2004; Garner et al., 2006; Lumeij and Hommers, 2008) have focused their attention on aetiologic factors, and have identified the importance of environmental enrichment (social housing, foraging opportunities and increase of physical complexity). It should be noted that most of these studies involved Amazon parrots rather than Grey parrots or cockatoos, which are the species most prone to develop FDB (Chitty, 2003a; Seibert, 2006b). Especially since the social structure and living environment are considered to vary among the different parrot species (e.g. May, 1996; Doneley, 2003; Seibert, 2006a), some caution should be taken when extrapolating these results to other species. Research has also provided an obvious link between rearing conditions and rearing methods and the onset of behaviour problems in parrots (e.g. Schmid, 2004; Luescher and Sheehan, 2005; Schmid et al., 2006). Additionally, Garner et al. (2006) showed involvement of genetics in the onset of FDB in Amazon parrots. Similar aetiologies (disturbed family relations,

Table 1
Comparison of the main characteristics of three behavioural disorders (feather damaging behaviour in parrots, trichotillomania in humans and feather pecking in laying hens).

	Feather damaging behaviour in parrots	Trichotillomania in humans	(Severe) feather pecking in laying hens
Phenomenology			
Primary focus	Self-plucking Sometimes other birds	Self-plucking Sometimes other people, objects or pets	Plucking of other birds Sometimes self-plucking
Tool	Beak	Hand & fingers	Beak
Location	Mainly chest, ventral side of wings, inner thighs Head in other birds	Hair of the scalp, eyebrows, eye lashes, moustache or beard, sometimes pubic hair	Mostly neck, back or vent
Demographic features			
Age of onset	Sexual maturity?	Puberty	Onset of lay
Cyclic changes	Yes	Yes	?
Sexe	Female-biased?	Female-biased?	Hens
Comorbid disorders	Yes?	Yes	?
Motivational systems			
Redirected foraging	Yes	No	Yes (particular severe FP)
Redirected dustbathing	No	No	Yes (gentle and severe FP)
Social function	?	No	Yes (gentle FP)
Tension release/Coping strategy	Yes	Yes (focused pulling)	Yes (gentle FP)
Abnormal repetitive behaviour (ARB)	Yes	Yes	Yes (gentle FP, also severe?)
Aetiological factors			
Genetic	Very likely	Suspected	Yes
Social	Hand-rearing, poor socialization, social isolation	Disturbed family relations, abuse in early childhood	Group size & density, social rank
Environment	Deprived environment, sudden changes	Poor education and income	Deprived environment; also light, feed composition
Physical	Various medical conditions	Scalp or hair injuries, lice	?
Neurobiological	Suspected	Suspected involvement of corticostriatal circuits (SAS), serotoninergic system	High dopamine, low serotonin; corticostriatal circuits
Triggers and cues			
Features of the plucked hair or feathers	Damaged feathers	Texture, shape, colour, symmetry of the hair	Damaged feathers, feather colour, particles
Situations	?	Situations with low (boredom) or high (tension) arousal	?
Therapeutic modalities			
Behavioural intervention			
Environmental enrichment	+	?	+
Foraging enrichment	+	?	+
Positive & negative reinforcement	+	+	?
Awareness strategy	?	+	?
Pharmacological intervention			
Tricyclic antidepressants	+	+	?
SRI's	+[a]	±	?
Dopamine agonists	+[a]	+[a]	+
Opioid antagonists	+[a]	+[a]	?
GnRH agonists/Sex hormones	+[a]	?	+[a]
Minor tranquilizers, anxiolytics	+[a]	+[a]	?
Dietary changes (e.g. tryptophan)	?	?	+
Genetic selection	? (not feasible)	not feasible	+

Table 1 Comparison of phenomenology, demography, aetiology, triggering cues, motivations and treatment modalities of feather damaging behaviour, trichotillomania and feather pecking.
? = Not investigated (yet).

[a] Suspected, based on favourable results, but not proven in placebo-controlled, randomized clinical trials.

abuse during childhood, poor financial state, genetics) can also be distinguished in TTM (e.g. Lenane et al., 1992; Lochner et al., 2002; Wright and Holmes, 2003; Woods et al., 2006b). However, in parrots FDB has often been loosely associated with a variety of medical conditions (Davis, 1991; Rosenthal, 1993; Juppien, 1996; Gylstorff and Grimm, 1998; Low, 2001; Seibert, 2006b). In humans these associations are rare (Christenson and Mansueto, 1999), and this may indicate an important distinction between the two disorders. However, in many instances, there is merely mention of an association rather than causal relationship. Additionally, it is difficult to distinguish normal preening from FDB (Van Hoek and King, 1997), let alone distinguishing FDB resulting from psychological issues from FDB due to pain or itching. This suggests that FDB represents a heterogeneous collection of disorders. Findings in support of this hypothesis were made by Garner et al. (2008), who identified at least two different groups of feather picking parrots (i.e. associated with immunologic/inflammatory disease or associated with trauma) based on histopathological features of paired skin biopsies.

The phenomenology of FDB and TTM also appear strikingly similar. In both, repeated plucking of hair or feathers occurs from specific body parts which is mainly directed at the individual itself, although some plucking of other conspecifics occurs (e.g. Christenson and Mansueto, 1999; Nett and Tully, 2003; Lightfoot and Nacewicz, 2006). Two key differences, however, should be noted, i.e. (1) birds pluck with their beak, whereas people with TTM pluck manually, and (2) TTM mainly involves plucking of hair on the scalp (e.g. Christenson et al., 1991b), whereas in parrots plucking is usually directed at the chest, ventral wings and/or inner thighs (e.g. Rosenthal, 1993; Nett and Tully, 2003). These differences may be (partially) explained by biological facts, i.e. most of the body in humans is hairless and plucking is therefore concentrated mainly on the head, whereas both plucking and grooming by parrots cannot involve of their own head as it is performed orally (Lefebvre, 1982; Harisson, 1986; Westerhof and Lumeij, 1987). It is, however, interesting to find that the plucking is sometimes directed at other birds, which is then predominantly aimed at the head of the conspecific (Lightfoot and Nacewicz, 2006).

The demographic features of FDB and TTM (age of onset (i.e. puberty or sexual maturation) and gender predisposition (female > male)) appear similar for FDB and TTM (e.g. Wedel, 1999; Du Toit et al., 2001; Garner et al., 2006), strengthening the case for the two disorders being similar. However, the knowledge on demography of FDB is mainly derived from observations in the field and experimental studies with small groups of animals. Larger epidemiological surveys are thus necessary to confirm these results. In addition, it is worth noting that a high proportion of birds and humans also appear to suffer from co-morbid disorders, such as neophobia/anxiety disorder, stereotypies or compulsive disorders (e.g. Christenson et al., 1991b; King et al., 1995; Meehan et al., 2003a; Schmid, 2004; Luescher and Sheehan, 2005; Garner et al., 2006).

One of the more striking differences can be found in the motivational backgrounds of both disorders. In parrots, great emphasis is placed on the function of the behaviour as 'adaptive' to its environment. It has been suggested to embody 'redirected foraging' resulting from lack of foraging opportunities (e.g. Meehan et al., 2003a,b; Lumeij and Hommers, 2008), but may also be considered as a 'coping strategy' as a result of stress or inadequate environment (e.g. Garner et al., 2006). Such 'coping strategies' have also been proposed for TTM (Diefenbach et al., 2002, 2008; Penzel, 2003), but only in rare instances a 'relief' is experienced after execution of the task. Furthermore, it most often occurs out of awareness of the individual, and is suggested not to serve an emotional regulatory role (Christenson and Mansueto, 1999). This led to the assumption that TTM should be considered as 'abnormal repetitive behaviour', more specifically an impulse control disorder, with concurrent pathology of certain brain regions (DSM-IV, Anonymous, 1994). It is thus questionable, if both disorders are similar in their neurobiological mechanisms, whether FDB actually comprises a coping function. Alternatively, psychoanalytical theories have suggested that TTM may be triggered or exacerbated by stressful situations that resonates with conflicts and symbols that inhabit the patient's unconscious mind (Koblenzer, 1999).

Finally, responses to behaviour therapy and efficacy of psychopharmacologic intervention have been documented more extensively in the last decade. In this context, the research conducted on the tricyclic antidepressant clomipramine seems promising, although it should be used with caution because of side-effects. Similar responses, both in intensity and duration, have been noted for TTM and FDB (e.g. Swedo et al., 1993; Grindlinger and Ramsay, 1994; Ninan et al., 2000; Seibert et al., 2004). The similarities in the response to clomipramine and (lack of) response to other drugs may indicate the presence of a common underlying neurobiological mechanism.

Some obvious similarities and differences in phenomenology, demography and aetiology of TTM and FDB thus exist. It would be of value to further address these similarities and differences via epidemiologic surveys and methodological experimental research. This will aid in the attempt to gain 'face validity' (i.e. similarity in phenomenology, demography and aetiology) of FDB as a model for TTM, similar to the study of Garner et al. (2004) in which he suggested barbering in mice as a spontaneous model for human trichotillomania. A good model, however, should not only have face validity, but preferably also encompasses 'predictive validity' (i.e. similarity in responses) and 'construct validity' (i.e. similarity in construction of the systems) (Moon-Fanelli et al., 1999). Construct validity warrants the need for neuroanatomical, neurochemical and functional studies. To address these issues and target a specific area in the brain, the type of perseveration that is present in parrots with FDB must be identified. Unlike parrots with stereotypy, which show 'recurrent perseveration' similar to autism (Garner et al., 2003), it is hypothesized that parrots with FDB show a 'stuck-in-set' perseveration. This type of perseveration has been well established in people with impulse control disorders, such as TTM (Rettew et al., 1991), and would indicate involvement of the prefrontal cortex. If–in analogy to people with TTM–a 'stuck in set' perseveration is found in parrots with FDB, renaming this disorder to 'pterotillomania', a term which emphasizes its compulsive nature (Lumeij and Hommers, 2008), would be favourable.

7.2. *Comparison of FDB and FP–what can studies in feather pecking hens teach us about feather damaging behaviour in parrots?*

In contrast to the many observed similarities with TTM, a number of apparent differences can be found between the phenomenology of FDB in parrots and FP in laying hens. FP in laying hens initially seems to be aimed at conspecifics rather than the bird itself, and targets other body areas (Wennrich, 1975). In fact, the only striking similarity seems to be that plucking in both instances occurs with the beak. However, some self-plucking has also been reported in laying hens (Blokhuis, 1986). Additionally, it needs to be emphasized that the method of housing may be of influence as well, i.e. laying hens are almost always housed in larger groups (Savory, 1995), whereas parrots in captivity are usually kept individually (e.g. Seibert, 2006b). The two seemingly different disorders might thus not be as different as one would initially think as housing may (in part) be held accountable for these differences in phenomenology.

Evidence to support the theory that FDB and FP are analogous behaviours can be found when comparing the demography, aetiology and motivational theories of the two disorders. Both occur at the same age (onset of lay, sexual maturation) and share a similar gender predisposition (female > male) (e.g. McKeegan and Savory, 2000; Garner et al., 2006). Second, a variety of similar social and environmental factors have been implicated in the prevention and onset of these behavioural disorders. The complexity of the (social) environment at a young age is critical, as demonstrated by McAdie and Keeling (2002), Chow and Hogan (2005) and Newberry et al. (2007). Research by Colette et al. (2000), Meehan et al. (2003b) and Fox and Millam (2004) indicated that behaviour development in young parrots is influenced by similar factors as in chickens. All of these studies provided support for the hypothesis that environmental enrichment at a young age will decrease fearfulness, and may be important in the development of coping strategies to stress, reduction of anxiety, and may subsequently also influence FDB. Rearing of chicks with a foster mother can also help to reduce FP (Riber et al., 2007; Rodenburg et al., 2009), similar to observations made by Schmid (2004) and Schmid et al. (2006). These analogies are further emphasized by the efficacy that has been demonstrated from environmental enrichment (increase of social, foraging, locomotor and/or physical opportunities) in the treatment of both disorders (e.g. Huber-Eicher and Wechsler, 1998; Meehan et al., 2003a,b; McAdie et al., 2005; Lumeij and Hommers, 2008). The similarities in aetiological factors have also suggested analogies in motivational background. In particular the 'redirected foraging' hypothesis has received growing attention by researchers in the field of FP, particularly in cases of severe FP (Huber-Eicher and Wechsler, 1998; Newberry et al., 2007), and has also been proposed in parrots with FDB (Meehan et al., 2003a; Lumeij and Hommers, 2008). 'Coping strategies' (particularly gentle FP, which may additionally serve a social function) and primary brain dysfunction leading to onset of abnormal repetitive behaviour, have also been proposed for both disorders (e.g. Korte et al., 1997, 1999; Van Hierden, 2003; Garner et al., 2006). The amount of evidence to support these hypotheses is more scarce for FDB as this has received little research relative to FP in laying hens.

7.3. *Future considerations*

In analogy to chickens (Van Hierden, 2003), neurobiological studies may be set up to identify the role of various hormones and neuropeptides (dopamine, serotonin, endorphins, ACTH, corticosterone) in the onset of the disorder. Confirmation of changes in levels (lack or excess) of these substances could provide additional evidence for a similar mechanism, and promote the use of specific psychopharmacological intervention in controlling the disorder. Addition of the serotonin precursor tryptophan to the food, as shown by Van Hierden et al. (2004b), could prove to be of particular interest, although the positive effects of other dietary supplements (essential amino acids and minerals) make its specific action as serotonin precursor questionable. Other hormones, such as corticosterone (or in general the hypothalamus–pituitary–adrenal (HPA) axis) may also be of interest. Differences in faecal corticosterone levels have been found between feather picking and non-picking Grey parrots (Owen and Lane, 2006). Alternatively, the influence of sex hormones on FDB would be worth investigating, as was suggested from results in humans (Keuthen et al., 1997) and laying hens (Hughes, 1973).

Similar to chicken, certain genetic markers may be involved as suggested by Garner et al. (2006). QTL studies, as performed in laying hens, might also be a good method for detecting increased risks for FDB and TTM, so that preventive actions can be undertaken. However, identification may prove to be difficult, as for many parrots a family history is not known. Genetic selection might be a valuable way to reduce FDB within the parrot population. Unfortunately implementation of such a programme will not be easy in the current breeding situation, although newer molecular genetic techniques might be of value to establish DNA profiles for purpose of parentage verification.

Other treatment modalities are of great interest for veterinarians and behaviourists confronted with FDB. To test the efficacy of the different strategies that have been proposed, case-controlled, randomized (multicenter) clinical trials should be set up, preferably in conjunction with research conducted in humans and laying hens. For these purposes both laboratory experiments and clinical trials with privately owned birds may be carried out. These trials may include strategies concerning environmental enrichment in analogy to the work on chickens (and work previously performed by Meehan and Mench, 2002; Meehan et al., 2003a,b, 2004; Garner et al., 2006), as well as strategies concerning behaviour therapy and psychopharmacological intervention, as used in TTM. Proper evaluation of treatment efficacy requires the use of reliable feather scoring methods. For this purpose, it is essential that the scoring systems (in case of FDB the scoring system as designed by Meehan and Mench, 2002) are validated first, by establishing intra- and inter-researcher coefficients of variation. Alternatively, new, more objective scoring methods may be developed.

Cross-sectional studies, as conducted in human medicine, from the population at large, may additionally help to obtain true prevalence values and predisposing factors, and subsequently help to gain a better insight in the possible risk factors that should be considered. Additionally, experimental studies may be conducted to indicate the importance of the different social and environmental factors that have been implicated to influence the onset of FDB. 'Consumer demand' studies may be found particularly suitable for such goals, as they help to assess and establish the bird's priorities, and indicate where preventative and therapeutic interventions should be aimed at (e.g. Mason et al., 1998; Cooper and Mason, 2001). Additionally, demonstrating the importance of foraging enrichment as a 'behavioural need' rather than 'time consumption', as is hypothesized in the 'contra-free loading' concept (Inglis et al., 1997), would lead to results in favour of the 'redirected foraging' hypothesis.

Subsequently, a relationship between the influence of these environmental variables, which may lead to onset of FDB or other grooming disorders (Spruijt et al., 1992), and the neurobiological changes, should be established. Particularly grooming behaviours, which are sited in the mesolimbic system, have been implicated as behaviours that occur when an individual is experiencing stress resulting from an inadequate environment or aversive stimuli. As a result, neuropeptide receptors (dopamine, serotonin) in the mesolimbic system are sensitized. This in turn is believed to lead to an increase in behaviours that are considered as 'self-rewarding' (such as grooming), in an attempt to restore the disrupted balance (Van der Harst, 2003; Cabib, 2006).

In conclusion, it should be stated that FDB, TTM and FP, are multifactorial in origin. Various developmental, social, environmental, hormonal, genetic and neurochemical factors are involved. An integrated and multi-faceted approach is thus needed to combat the disorders. This review shows that these disorders share many of the same characteristics and involve similar underlying mechanisms. However, based on the information available, the question whether these disorders are really the same (i.e. presence of 'predictive' and 'construct validity'), or merely appear the same (i.e. 'face validity'), remains to be answered.

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