Feather pecking and related behavioural characteristics in laying hens

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Feather pecking and related behavioural characteristics in laying hens

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“Een heer weet soms meer dan hij denkt”

Olivier B. Bommel

Voor mijn vader
Voor Oom Arie

Abstract

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Feather pecking is a major welfare and economic problem in laying hens. It is characterised by pecking at- and pulling out of feathers of conspecifics. A bird's propensity to develop feather pecking may be related with other behavioural characteristics, such as reaction to frustration (the omission of expected reward) and social motivation. Furthermore, differences in feather pecking between lines indicate that genetic background plays an important role.

In this thesis, the relationship between feather pecking and other behavioural characteristics was studied in two lines that differed in feather pecking behaviour: the high (HFP) and low (LFP) feather pecking lines. The importance of the social environment was evaluated in an experiment where different tests to measure feather pecking were compared. Furthermore, the reaction to frustration was studied in these lines and it was studied whether frustration can facilitate feather pecking directly. In a behaviour genetics study, it was studied whether behavioural traits measured at young age were predictive of feather pecking at adult age.

It was found that the social environment plays an important role in the development of feather pecking. Pecking at a bunch of feathers in an individual context is not comparable with feather pecking in a social group. Although HFP and LFP lines showed differences in reaction to frustration, short-term frustration in a Skinnerbox could not facilitate feather pecking. Finally open-field behaviour at young age was found to be predictive of pecking behaviour at adult age. These results were used to develop a model on the relationship between feather pecking and other behavioural characteristics, that may be helpful to solve the problem of feather pecking in laying hens.

Contents

Voorwoord

Voor u ligt het resultaat van vier jaar kippenonderzoek. Vier jaar waarin ik veel heb geleerd en veel heb gelachen. Als kippenonderzoeker ben je vaak het middelpunt van de borrelpraat, met titels variërend van kippendokter, of hij-die-met-kippen-praat, tot kippenpsycholoog. Op een gegeven moment was mijn ster zelfs zover gerezen dat ik met een kippenspandoek werd afgehaald van Schiphol (het precieze opschrift kan ik me niet herinneren).

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Bas
Heelsum, augustus 2003

Chapter 1
General Introduction

Abnormal behaviour

Domestication of wild animals and the development of animal husbandry have caused major changes in the animal's situation. Animals kept in captivity have a sufficient supply of food and water and protection from diseases, predators, and weather influences, whereas wild animals have to search for food and water and live in a less protected environment. On the other hand, captive animals often have limited space and limited behavioural possibilities (Newman, 1994). These restrictions may result in abnormal behaviour. Houpt (1987) defined abnormal behaviour as: 'a novel behaviour or an otherwise normal behaviour that is exaggerated in terms of frequency or intensity, disoriented in relation to the stimulus, or occurring in the absence of normal eliciting stimuli'. Abnormal behaviour can also be defined as behaviour that is neither natural, nor functional. The occurrence of abnormal behaviour can often be attributed to the restricted environment in which the animals are kept (Sambraus, 1985). Abnormal behaviour may cause damage to the animal itself or its conspecifics. Self damaging behaviour is seen in parrots in the form of self-pecking, when a bird chews and pulls out its own feathers. Factors influencing self-pecking in parrots are social isolation, lack of environmental stimulation and inadequate diet (Meehan et al., 2003). Tail biting in pigs (Schrøder-Petersen and Simonsen, 2001) is an example of a behaviour that leads to damage of conspecifics. Tail biting is suggested to be either a learned response, a natural behaviour displayed with increased intensity or a redirected behaviour (Schrøder-Petersen and Simonsen, 2001). Feather pecking in laying hens also leads to damage of conspecifics. Feather pecking is a major economic and welfare problem in laying hens, as well as in other birds kept in captivity such as ducks, Japanese quail, pheasants and ostriches (Hoffmeyer, 1969; Bilcík and Bessei, 1993; Raud and Faure, 1994; Sambraus, 1995). It results in extensive feather damage, higher feeding costs due to heat loss and increased mortality rates (Blokhuis and Wiepkema, 1998). In this thesis feather pecking and related behavioural characteristics will be studied and findings will be related to abnormal behaviours found in other species.

What is feather pecking?

Feather pecking in laying hens can be characterised as pecking at and pulling out of feathers of conspecifics. Different types of bird-to-bird pecking can be distinguished. In a workshop at the 9th European Poultry Conference in Glasgow (1994) a classification of pecking behaviour was proposed categorising five types of bird-to-bird pecking based on both cause and effect (Savory, 1995). The five types distinguished were (1) aggressive pecking, (2) gentle feather pecking without removal of feathers, (3) severe feather pecking leading to feather loss, (4) tissue pecking in denuded areas and (5) vent pecking (Figure 1.1).

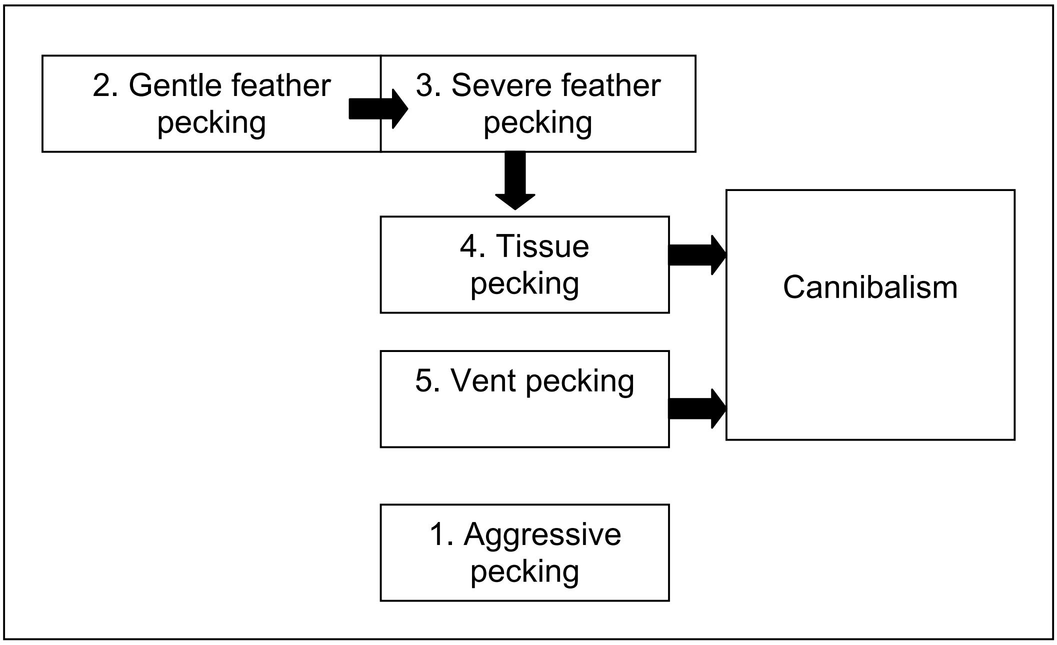

Figure 1.1 Forms of bird-to-bird pecking (classification after Savory, 1995).

Aggressive pecking is used to establish a stable dominance hierarchy. It may lead to some damage to the head and neck region, but it should not be confused with feather pecking behaviour. Feather pecking without removal of feathers, or gentle feather pecking, sometimes appears to be directed at litter particles on the plumage, but can also develop into stereotypic pecking with a high frequency. It can cause some damage but is often ignored by the recipient. Severe feather pecking, or feather pulling, is characterised by forceful pecking at- or pulling out of feathers, to which the victim usually reacts.

Feathers that are pulled out are sometimes eaten. It causes feather damage and can lead to bald patches. These bald patches may attract tissue pecking, which can result in wounding of the victim and cannibalism, i.e. the consumption of flesh or blood. Vent pecking is often seen around the onset of lay and is directed at the prolapsed uterus and the feathers around it. Vent pecking may start as investigatory pecking, but can also lead to cannibalism when the uterus is damaged or the internal organs are pulled out. A last form of bird-to-bird pecking is beak pecking (not shown in Figure 1.1). Beak pecking is characterised by gentle pecking at the beak of another bird. The pecker approaches the other bird from below. It is often observed around the feeder and is directed at food particles on the beak of the other bird. Gentle feather pecking, severe feather pecking and tissue pecking are not completely clear-cut and may grade into each other (Savory, 1995). In a recent paper, McAdie and Keeling (2002) suggested that, in adult laying hens, gentle feather pecking may develop into stereotyped gentle feather pecking and severe feather pecking by either increased frequency or increased severity of bird-to-bird pecks. If this is indeed the case, gentle feather pecking early in life may be a good indicator of severe feather pecking in adult laying hens.

Causation of feather pecking

Feather pecking is thought to be a form of redirected behaviour, developing either from ground pecking (Blokhuis, 1986) or pecking during dustbathing (Vestergaard and Lisborg, 1993). Blokhuis and Arkes (1984) showed that birds housed on slatted floors showed more feather pecking and less ground pecking than birds housed on litter. Moreover, when birds housed on litter were transferred to slatted floors, feather pecking increased in these birds. These results support the hypothesis that ground pecks are redirected at feathers when no substrate is available (Blokhuis and Arkes, 1984). Vestergaard and Lisborg (1993) showed that chicks that are trained to dustbath on feathers instead of sand, continued to dustbath on- and peck at feathers later in life, even if they could choose between sand and feathers. It was proposed that chicks that miss early experience with substrates as sand or peat for dustbathing may develop a preference for feathers as a pecking and dustbathing substrate (Vestergaard et al., 1993). Huber-Eicher and Wechsler (1997), however, showed that provision of sand did not prevent feather pecking, whereas the provision of straw led to a reduction of feather pecking. Furthermore, feather pecking was inversely related with foraging activity, but not with dustbathing activity (Huber-Eicher and Wechsler, 1997). In another study, Riedstra and Groothuis (2002) found evidence that early feather pecking can also be interpreted as social exploration, as unfamiliar birds were pecked more frequently than familiar birds. It remains unclear, however, how feather pecking at young age can be related to feather pecking at adult age.

Environmental factors

Environmental factors that influence the development of feather pecking are floor substrate availability and quality (as discussed above), group size and stocking density, food form, light intensity and colour, and rearing conditions. In large groups more feather pecking was observed than in small groups (Allen and Perry, 1975), whereas Savory et al. (1999) found most feather damage in large groups with a high stocking density. Feather pecking is observed in cages as well as in large group-housing systems (Appleby and Hughes, 1991). In large group-housing systems, however, the problem is more difficult to control, as feather pecking may spread by social transmission (Zeltner et al., 2000). Furthermore, food form affects feather pecking. Birds that were fed pellets showed more feather pecking than birds fed mash (Aerni et al., 2000). Kjaer and Vestergaard (1999) showed that light intensity affected feather pecking. Gentle feather pecking developed more often in groups with a low light intensity, whereas severe feather pecking was seen more under high light intensity. Light colour may also play a role, as D'Eath and Stone (1999) showed that light colour affects social recognition in laying hens. Rearing conditions may play an important role as well, especially the presence of a mother-hen is frequently mentioned. Roden and Wechsler (1998) showed that the presence of a hen during the rearing period increased activity of the chicks. They did not find a difference in feather pecking between birds from different rearing conditions, however.

Genetics of feather pecking

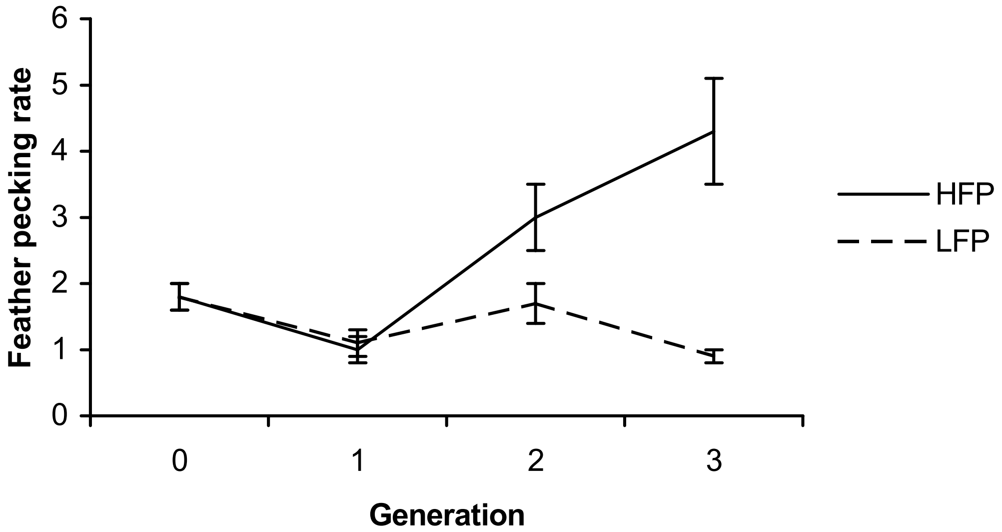

Figure 1.2 Feather pecking rate of founder White Leghorn line in generation P (corresponding to generation 0) and selection lines LP and HP in generations 1–3 (from Kjaer et al., 2001).

Line differences in plumage condition (Ambrosen and Petersen, 1997; Wahlstrom et al., 2001) and in feather pecking behaviour (Hughes and Duncan, 1972) suggest a genetic background. Selection against feather pecking has been shown to be feasible (Muir, 1996; Kjaer et al., 2001). They successfully used individual selection on feather pecking behaviour to create a high and a low feather pecking line (Figure 1.2). Muir (1996) used group selection to reduce problems with cannibalism. Mortality was reduced from 68% in generation 2 to 9% in generation 6 using group selection on production related traits (Muir, 1996).

Relationship with other behavioural characteristics

Frustration, i.e. the omission of expected reward, may play a role in the development of feather pecking. Duncan and Wood-Gush (1972) showed that frustration of feeding behaviour leads to high levels of pecking at the covered feeder and at other parts of the cage. Lindberg and Nicol (1994) supplied hens with operant feeders to reduce problems with feather pecking. They hypothesised that the birds would direct more pecks at the operant feeding devices and less at other birds. Unexpectedly, birds with operant feeders developed higher levels of feather pecking than birds with normal feeders.

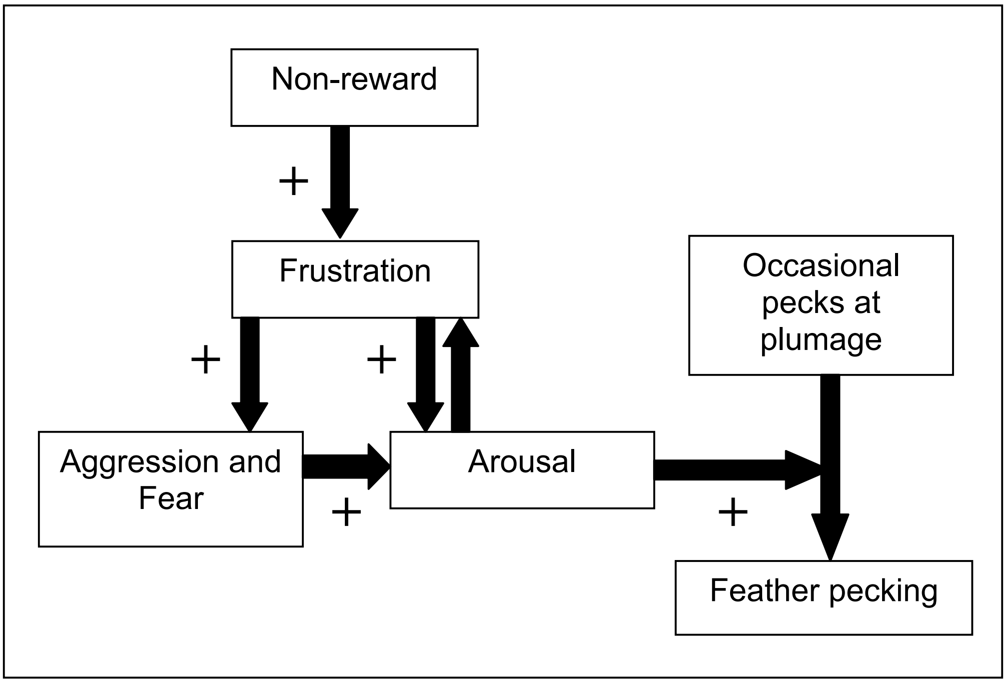

Figure 1.3 Proposed model on the role of frustration in the development of feather pecking (part of the model described in Lindberg and Nicol, 1994).

They proposed a model (Figure 1.3) in which frustration (defined here as feeling frustrated), for instance because a bird tries to reach the operant feeder but is unsuccessful, results in increased arousal, aggression and fear. Under these circumstances, occasional pecks at the plumage of other birds may develop into more damaging forms of feather pecking (Lindberg and Nicol, 1994). Taylor et al. (2001) studied the effect of giving birds operant control over food and light and found that groups with operant control did not show more feather pecking than control groups. In their study, however, groups consisted of only five birds, as compared to groups of 80 birds in the study by Lindberg and Nicol (1994). In the study by Taylor et al. (2001), each bird should be able to reach and operate the feeder, avoiding frustration and frustration-induced pecking.

Feather pecking has also been associated with fearfulness (Hughes and Duncan, 1972; Vestergaard et al., 1993), with open-field response (Jones et al., 1995) and with coping strategy (Korte et al., 1997).

Hughes and Duncan (1972) showed that birds in cages with the most feather damage also were the most fearful, whereas Vestergaard et al. (1993) actually showed that the birds performing feather pecking were most fearful, as assessed by their tonic immobility. Jones et al. (1995) showed that young chicks from a low feather pecking (LFP) line vocalised and walked sooner in an open-field than chicks from a high feather pecking (HFP) line and suggested that this reflects differences in social motivation to return to their flock-mates. Korte et al. (1997) showed that birds from these same HFP and LFP lines showed differences in stress response after manual restraint. LFP birds showed a stronger corticosterone response than HFP birds, whereas HFP birds showed a larger plasma noradrenaline response. From these results, Korte et al. (1997) suggested that these lines may have different coping strategies, as found in rodents: pro-active (fight/flight) and reactive (conservation/withdrawal) copers (Koolhaas et al., 1999). Korte et al. (1997) proposed that birds from the HFP line may be characterised as pro-active copers and birds from the LFP line as reactive copers (Korte et al., 1997).

High and low feather pecking lines

In this study, the high (HFP) and low (LFP) feather pecking lines that were also studied by Korte et al. (1997) and Jones et al. (1995) were used as a model to study feather pecking. These lines are selection lines from a commercial breeder in the Netherlands. They were selected for production related traits and also showed a consistent difference in feather pecking behaviour. As these lines also differed in stress response and open-field behaviour, they seemed a very good starting point to ask ourselves the question: is feather pecking related with other behavioural characteristics.

A model was proposed explaining the role of frustration in the development of feather pecking and the difference in effect of frustration between the HFP and LFP line. Following the model of Lindberg and Nicol (1994), we hypothesised that frustration leads to increased arousal, and that short-term and long-term frustration have a similar effect. Increased arousal leads to anxiety and aggression, measurable in open-field activity and aggressive pecking behaviour. Increased arousal will also result in a stronger pecking motivation.

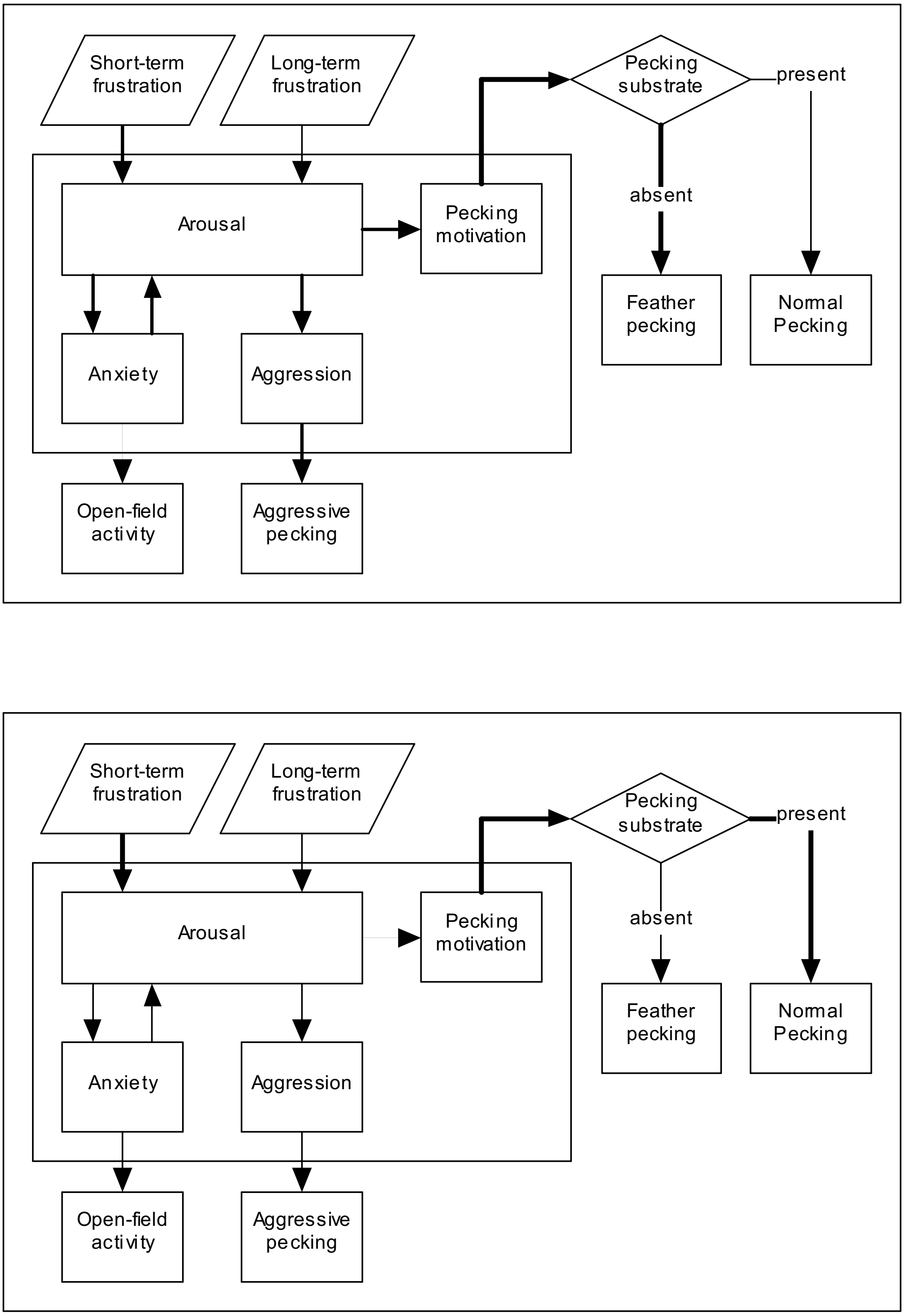

Figure 1.4 The role of frustration in the development of pecking behaviour in the HFP line (top panel) and in the LFP line (bottom panel). Bold arrows represent an increased intensity compared with normal arrows.

Depending on the availability of a pecking substrate, this results in normal pecking behaviours (with increased intensity) or in redirected pecking behaviour, resulting in feather pecking. In HFP birds (Figure 1.4 top panel), anxiety and aggression will increase stronger than in LFP birds (Figure 1.4 bottom panel), thus leading to increased fearfulness (reduced open-field activity), more aggressive pecking and a higher pecking motivation compared with LFP birds. Higher levels of anxiety will also lead to more arousal. Furthermore, HFP birds will show more feather pecking than LFP birds, whereas LFP birds will rather show increased levels of normal pecking, because HFP birds have a higher propensity to redirect pecking at feathers during frustration.

Aim and outline of the thesis

The project described in this thesis was part of a program on feather pecking in laying hens, consisting of four PhD-projects. Physiological characteristics of feather pecking were studied at ID-Lelystad, ontogenetic aspects at the University of Groningen, and molecular genetics (Animal Breeding and Genetics Group) and behavioural characteristics (Ethology Group) at Wageningen University.

The aim of this thesis was to study the behavioural characteristics of feather peckers and non-feather peckers, following the hypotheses described in the proposed model (Figure 1.4). In Chapter 2, we aimed to select an appropriate test to measure feather pecking in laying hens, comparing individual and social tests with pecking behaviour in the homepen. We hypothesised that pecking behaviour in the individual test would be influenced by a bird's behavioural characteristics, as shown in Figure 1.4. Furthermore, a bunch of feathers was expected to be an appropriate substrate to elicit feather pecking. Finally genetic (line) differences in propensity to develop feather pecking were supposed to be measurable at individual level, both at young and at adult age.

The role of frustration in the development of feather pecking was studied in Chapters 3, 4 and 5. In Chapter 3, reaction to frustration was studied in high and low feather pecking birds (both genetic and phenotypic). It was hypothesised that birds that showed more feather pecking would show a stronger reaction to frustration, reflecting their coping strategy. Furthermore, it was studied whether frustration could trigger pecking at a bunch of feathers. We hypothesised that feather peckers would be attracted to peck at the bunch of feathers during frustration. In Chapter 4, reaction to frustration in birds from commercial (reared in large group, no mother hen) or semi-natural (reared in small group, mother hen) rearing conditions were studied. Birds from semi-natural rearing conditions were expected to show less feather pecking than birds from commercial rearing conditions, as their individual characteristics were affected differently by early life experiences. This would influence both reaction to frustration and development of feather pecking. It was also studied whether frustration led to pecking at feathers fitted to one of the keys of the Skinnerbox, expecting that feather peckers would be attracted to peck at the feathers during frustration. In Chapter 5, it was studied whether frustration can trigger feather pecking directly. It was hypothesised that frustration could both serve as a trigger in birds that had already developed feather pecking and as an incentive to develop feather pecking in birds that had never shown feather pecking previous to the experiment, using repeated frustration sessions.

In Chapter 6 and 7, behaviour genetics of feather pecking and open-field behaviour were studied in an F_2 cross of high and low feather pecking lines. Aim of this study was to estimate heritabilities of feather pecking and identify possible predictors of feather pecking, preferably measurable at young age. We hypothesised that open-field behaviour and feather pecking at young age would be predictive of feather pecking at adult age.

In Chapter 8, the major findings of Chapter 2 - 7 will be discussed.

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Chapter 2
Comparison of individual and social feather pecking tests in two lines of laying hens at ten different ages

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Abstract

The aim of this experiment was to select a suitable test to measure feather pecking in laying hens. Pecking behaviour in individual and social feather pecking tests was compared with pecking behaviour in the homepen. Two lines of laying hens were used that differ in their propensity to display feather pecking: the high (HFP) and low (LFP) feather pecking lines. Six groups of five birds per line were housed on wood shavings with ad libitum food and water. From 7 to 34 weeks of age, every three weeks pecking behaviour in the homepen was observed and three feather pecking tests were conducted as well: one individual test with a bunch of feathers (10 minutes) and two social tests (in random order), one with and one without a bunch of feathers (30 minutes with whole group). Observations focused on gentle and severe feather pecking, bunch pecking, ground pecking and preening. In the individual test general activity and vocalisations were recorded as well, to measure the response to isolation.

In general, HFP birds showed more gentle and severe feather pecking than LFP birds, whereas LFP birds showed more ground pecking and, unexpectedly, more bunch pecking. Birds that showed gentle feather pecking in the homepen also showed gentle feather pecking and bunch pecking in the social tests over all ages. Severe feather pecking in the social test with a bunch of feathers corresponded with severe feather pecking in the homepen. Bunch pecking in the individual test was not a reliable measure for feather pecking in this experiment. An increasing number of vocalisations in the HFP line and a decreasing number in the LFP line indicated a difference in reaction to the individual test. In conclusion, gentle and severe feather pecking and bunch pecking in the social test corresponded best with homepen behaviour, whereas bunch pecking in the individual test did not.

Introduction

Different forms of bird-to-bird pecking in laying hens have been identified (Savory, 1995). Gentle feather pecking, or feather pecking without removal of feathers, causes little or no feather damage and is often ignored by the recipient. Severe feather pecking, or feather pulling, is more forceful and leads to feather damage and feather loss. Tissue pecking is directed at denuded areas. Severe feather pecking and tissue pecking can eventually result in cannibalism (Savory, 1995).

Feather pecking is thought to be a form of redirected behaviour, developing either from food pecking (Wennrich, 1974), ground pecking (Blokhuis, 1986) or pecking during dustbathing (Vestergaard and Lisborg, 1993). Savory and Mann (1999) suggested that food pecking, ground pecking and feather pecking are all substitutable. Recently, McAdie and Keeling (2002) suggested that damaging feather pecking may also develop from gentle feather pecking at an early age by increasing intensity (stereotyped gentle feather pecking) or severity (severe feather pecking) of the pecks.

Frustration may stimulate the redirection of pecking behaviour at feathers. Lindberg and Nicol (1994) proposed a model in which frustration, for instance because a bird tries to reach the feeder but is unsuccessful, results in increased arousal, aggression and fear. Under these circumstances, occasional pecks at the plumage of other birds may develop into more damaging forms of feather pecking (Lindberg and Nicol, 1994). Frustration may play a key role in the development of feather pecking.

The propensity to develop feather pecking behaviour may also be influenced by other individual characteristics, such as coping with stress and reactivity to the environment. The same high (HFP) and low (LFP) feather pecking lines used in this study, were shown to have a different behavioural and physiological characteristics (Jones et al., 1995; Korte et al., 1997; Van Hierden et al., 2002). In response to a manual restraint test, LFP birds had a stronger corticosterone response than HFP birds, whereas HFP birds had a larger plasma noradrenaline response. From these results, Korte et al. (1997) suggested that these lines may have different coping strategies, as found in rodents: pro-active (fight/flight) and reactive (conservation/withdrawal) copers (Koolhaas et al., 1999). Birds from the HFP-line may be characterised as pro-active copers and birds from the LFP-line as reactive copers (Korte et al., 1997). In agreement with this, LFP birds have also been shown to have a higher social motivation than HFP birds (Jones et al., 1995). Furthermore, Van Hierden et al. (2002) recently showed in young birds, that HFP birds showed more feather pecking and preening than LFP birds whereas LFP birds performed more ground pecking, indicating differences in reaction to the environment.

Both individual and social feather pecking tests have been used to measure feather pecking in laying hens. In a social test described by Kjaer and Sørensen (1997), pecking behaviour of a group of birds was observed. This test was used successfully to create feather pecking selection lines (Kjaer et al., 2001). In an individual test used by Bessei et al. (1997), the propensity of a caged hen to peck and pull at a bunch of feathers was measured. A positive correlation was found between severe feather pecking observed in the homepen and severe feather pecking recorded in the individual test (Bessei et al., 1997). Cloutier et al. (2000) studied whether pecking at inanimate stimuli is a predictor of cannibalism. They also used pecking at a bunch of feathers as a possible predictor of feather pecking. No correlations were found between pecking at the bunch of feathers and pecking at flock mates at a later age. A tendency was found for future cannibals to have a longer latency to peck the inanimate stimuli (Cloutier et al., 2000). From these results the question arises which test to use to measure a bird's propensity to develop feather pecking: a social or an individual test, measuring bird-to-bird pecking or pecking at a bunch of feathers. A reliable test of the propensity to develop feather pecking would be a valuable tool in future breeding programs intended to minimise the problems with feather pecking and feather damage.
The aim of the current experiment was to select an appropriate test to measure feather pecking in laying hens. Pecking behaviour in individual and social feather pecking tests was compared with pecking behaviour in the homepen in two lines of laying hens that differed in their propensity to display feather pecking.

In the different testing environments, a bird's coping strategy and its reaction to frustration (for instance during isolation) may influence pecking behaviour. Birds were not isolated from the group in the social tests. Therefore we expected the birds would not have a strong response to the testing procedure for these tests. In the individual test, isolation from the group might influence behaviour. To record possible line differences in response to this individual test, the behavioural response to testing was recorded in more detail.

Materials and methods

Animals and housing

Two White Leghorn selection lines from Hendrix Poultry Breeders, The Netherlands, were used for the experiment: the so-called high (HFP) and low (LFP) feather pecking lines. These lines have been selected for production related traits and the difference in feather pecking is a coincidental result of this selection program (Korte et al., 1997). There is still overlap in feather pecking behaviour between the HFP- and LFP-line (McAdie and Keeling, 2002). Birds arrived on the farm as day-old chicks in two batches, because the first batch did not contain enough LFP chicks. The first batch consisted of 30 HFP chicks and 15 LFP chicks. The second batch arrived one week after batch 1 and consisted of 15 LFP chicks. Hereafter the mean age of batch 1 and 2 will be taken as measure for age. From 0 to 3 weeks of age, HFP and LFP birds were reared separately on wood shavings in two rearing pens, measuring 1.5 x 1.5 m. At three weeks of age, six groups of five birds per line were housed in one of the twelve experimental pens. Birds from the LFP line were divided into three groups from batch 1 and three groups from batch 2. Pens measured 1.5 x 1.5 m, with wood shavings on the floor, two laying nests and a perch. Food and water were available ad libitum. From week 0 through week 4 birds had continuous light (2 heating lamps per pen). At five weeks of age light was on for 8 hours per day, from 8:00 until 16:00. Every week the light period was expanded with one hour. At 13 weeks of age light was on for 16 hours per day, from 3:00 until 19:00 and this stayed the same throughout the laying period. Light was supplied by 8 tubes (40 W each) distributed evenly over the ceiling of the experimental facility. At 15 weeks of age, an outbreak of coccidiosis occurred. Four birds per line died as a result of this infection. Hence, groups that were infected were not tested in the ex situ tests at 16 weeks of age. One HFP group was excluded from the experiment because only two birds were left. Birds were treated with vitamins and from 17 weeks of age onwards, no problems with coccidiosis were found anymore.

Behavioural tests and observations

From 7 to 34 weeks of age, every three weeks a test period was conducted (10 test periods in total). In each test period, pecking behaviour in the homepen was observed and three feather pecking tests were conducted as well: one individual test with a bunch of feathers (10 minutes) and two social tests, one with and one without a bunch of feathers (30 minutes with whole group). In each test period two days were used for behavioural observations, two days for the individual test (30 birds per day) and two days for the social tests (60 birds per day). Within each test period, the order in which the tests were performed was alternated.

During homepen observations, each pen was observed for 30 minutes once in the morning and once in the afternoon on each day. The order in which pens were observed was alternated between the two observation days. Behaviour sampling was used for the observations, focusing on pecking behaviour (see Table 2.1 for the ethogram). Only bouts of pecking behaviour were observed in the homepen, because five birds had to be observed simultaneously. A bout started when the bird started, for instance, ground pecking and ended when the bird stopped ground pecking for more than five seconds or started performing a bout of a different pecking behaviour. The three feather pecking tests were performed in a sound attenuated room, adjacent to the homepens, using a testing pen with hardboard walls and a Perspex wall measuring 1.25 x 1.25 m with wood shavings on the floor. Light was supplied by 2 tubes (40 W each), resulting in a higher light intensity in the test pen than in the homepens. Birds had no access to food, water, perches or laying nests in this area. All five birds from one group were transported from the homepen to the testing pen in a plastic crate. They were placed in the testing pen in darkness. Then the light was switched on and the experimenter left the room. Observations started at the moment the door was closed. Behaviour was recorded on video using a video camera, placed in front of the Perspex wall, and an external microphone, attached above the testing pen. Videotapes were analysed later using The Observer® programme (Noldus, 1993).

Table 2.1 Ethogram used for data recording in the homepen (H), the social test without (S) and with (S^+) a bunch of feathers and the individual test (I^+).

Behaviour	Description	H	S	S^+	I^+
Aggressive pecking	Forceful pecks, directed at head or neck region	X	X	X	
Gentle feather pecking	Gentle pecks, ignored by recipient	X	X	X	
Gentle feather peck	Singular gentle peck within a bout		X	X	
Severe feather pecking	Forceful pecks, reaction receiver	X	X	X	
Severe feather peck	Singular severe peck within a bout		X	X	
Bunch pecking	Pecking at the bunch of feathers			X	X
Bunch peck	Singular bunch peck within a bout			X	X
Ground pecking	Pecking at the floor	X	X	X	X
Wall pecking	Pecking at the walls	X	X	X	X
Preening	Preening own feathers		X	X	X
Dustbathing	Dustbathing, lying on floor		X	X	X
Vocalising	Note of vocalisation				X
Walking	Time spent walking				X

The bunch of feathers used in the behavioural tests consisted of 10 white tail feathers, 10 to 15 cm in length. Feathers were given a scruffy appearance, as this has been shown to attract feather pecking (McAdie and Keeling, 2000). These feathers were fitted in a plastic tube, which was fixed in the floor of the test pen, near the Perspex wall. About 10 cm of the length of the feathers protruded from the tube. The tube was presented in sight of the birds and the feathers were presented vertically at bird height, resembling the tail of a bird.

For both social tests behaviour sampling was used, focusing on pecking behaviour (see Table 2.1 for the ethogram). Focal sampling was used for the individual feather pecking test. A more detailed ethogram was used for these observations, including general activity and vocalisations (Table 2.1), to measure the behavioural response to testing. At 7 weeks of age, the social test with a bunch of feathers was omitted, due to problems with the time schedule.

Analysis

Data were analysed using analysis of variance in the SAS® statistical programme (SAS, 1996). Frequencies of all observed behaviours were transformed with a square root transformation, because data were not distributed normally. Repeated measures analysis of variance was used for the analysis. The model included line and group. Line nested in group was used as error term. In a preliminary analysis of the data, no major differences were found between the two batches of LFP-birds, so batch was removed from the model. Orthogonal polynomial contrasts were used to compare pecking behaviour at the different ages in a trend analysis (Sokal and Rohlf, 1969, pp. 468-476). To study the validity of each behavioural test at an individual level, birds were characterised as peckers (>0 bouts) or as non-peckers (0 bouts) in each of the behavioural tests at each age. This characterisation was compared with each bird's genetic (line) and phenotypic (homepen behaviour) information using the simple kappa coefficient (SAS, 1996). It was hypothesised that (1) birds from the HFP-line would show more feather- and bunch pecking in all tests and that (2) birds that were characterised as peckers in the homepen would also show feather- and bunch pecking in each test. A combined probability was calculated over all ages using the hypotheses mentioned above, although tests are not completely independent (same birds at different ages), using Fisher's method (Sokal and Rohlf, 1969, pp. 621-624).

Results

In the homepen, HFP birds showed more gentle feather pecking over all ages than LFP birds ($F_{1,9}$=8.03; $p<0.05$; Figure 2.1). In both social tests, no line differences over all ages were found for gentle feather pecking. In the social test without a bunch of feathers, HFP birds showed more gentle feather pecking than LFP birds at 7 weeks of age ($F_{1,9}$=27.09; $p<0.001$). At 16 and 19 weeks of age, however, LFP birds showed more gentle feather pecking than HFP birds in both social tests. A linear decrease of gentle feather pecking over age was found in both the homepen ($F_{1,9}$=118.97; $p<0.001$), the social test without ($F_{1,9}$=31.99; $p<0.001$) and with ($F_{1,8}$=12.40; $p<0.01$) a bunch of feathers (Figure 2.1).

Levels of severe feather pecking were low. Over all ages, HFP birds showed more severe feather pecking in the homepen than LFP birds ($F_{1,9}$=10.78; $p<0.01$; Figure 2.2). A comparable difference in severe feather pecking over all ages between lines was found in the social tests without ($F_{1,9}$=6.33; $p<0.05$) and with ($F_{1,8}$=5.61; $p<0.05$) a bunch of feathers. In this test, a line difference was found in the trend analysis, with a linear increase of severe feather pecking over age in the HFP-line, but not in the LFP-line ($F_{1,9}$=11.97; $p<0.01$).

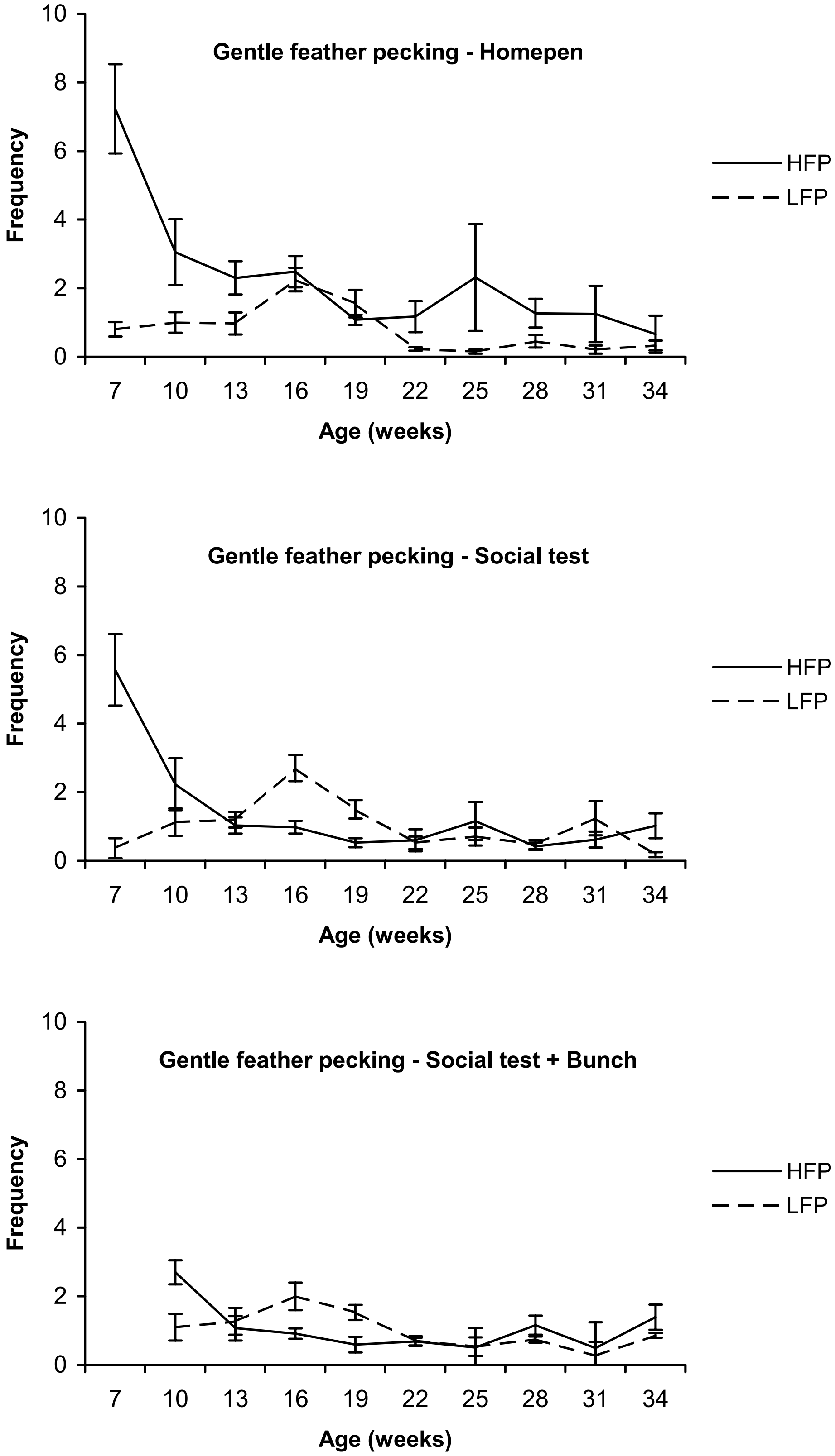

Figure 2.1 Mean number of bouts of gentle feather pecking over time in the homepen (top panel) and the social tests without- (middle panel) and with (bottom panel) a bunch of feathers in the HFP and LFP lines.

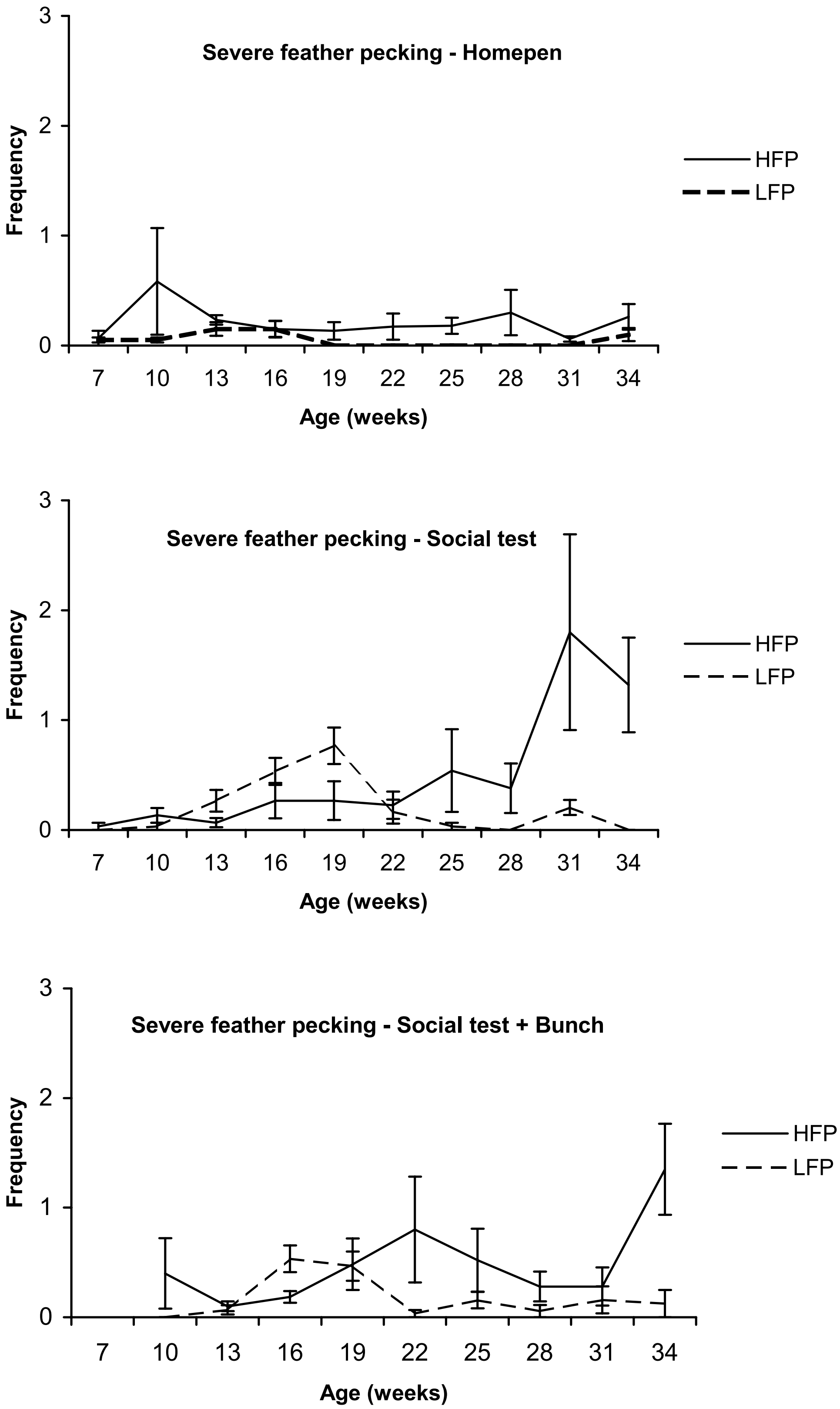

Figure 2.2 Mean number of bouts of severe feather pecking over time in the homepen (top panel) and the social tests without- (middle panel) and with (bottom panel) a bunch of feathers in the HFP and LFP lines.

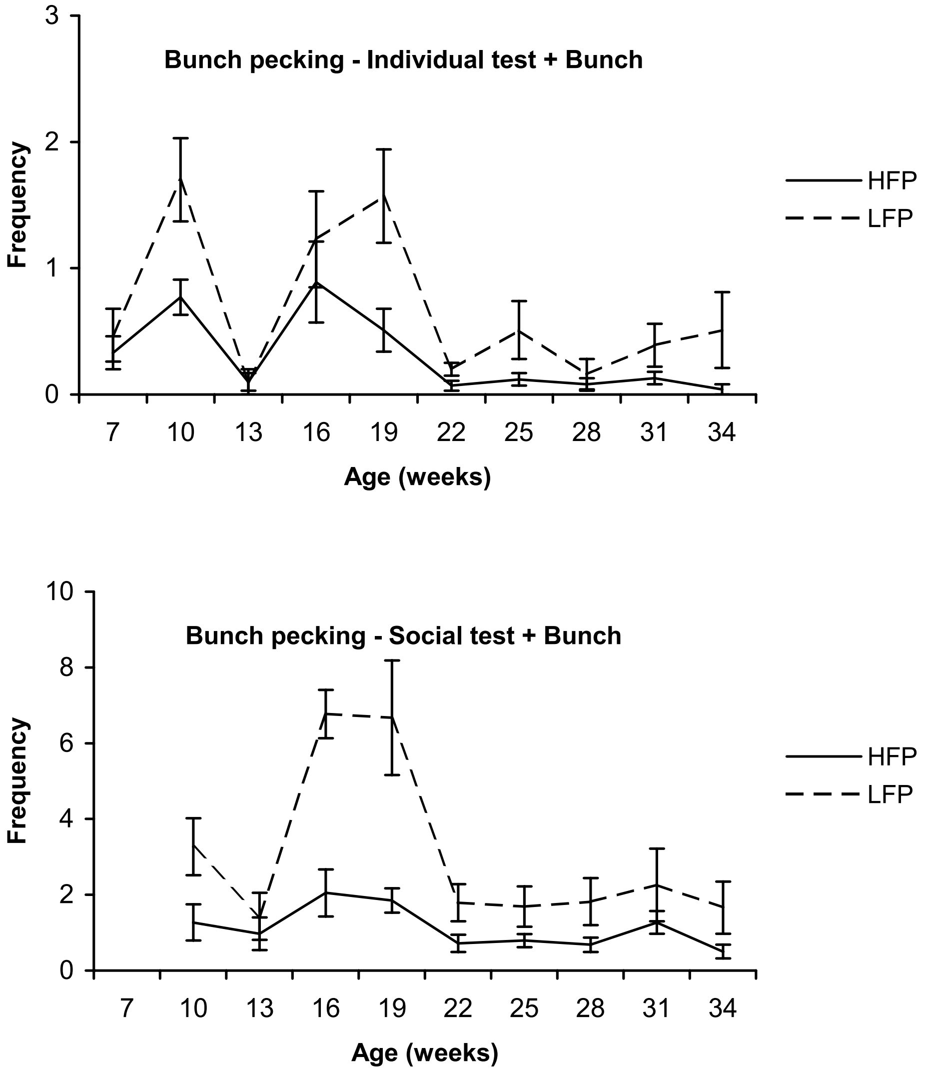

Figure 2.3 Mean number of bouts of bunch pecking over time in the individual test (top panel) and in the social test with- (bottom panel) with a bunch of feathers in the HFP and LFP lines.

In the social test with a bunch of feathers, LFP birds showed more bouts of bunch pecking behaviour over all ages than HFP birds ($F_{1,8}$=7.09; $p<0.05$; Figure 2.3). The LFP birds showed relatively high levels of bunch pecking at 16 and 19 weeks of age. In the individual test line differences were not significant ($F_{1,10}$=0.60; p=0.46). In this test also a linear decrease of bunch pecking over age was found ($F_{1,10}$=5.26; $p<0.05$).

For validation purposes, it was tested whether birds that showed gentle and severe pecking in the homepen also showed feather or bunch pecking in each of the tests at each age (Table 2.2).

Table 2.2 Simple kappa coefficients of agreement (ranges from -1 to 1) for gentle feather pecking (gent), bunch pecking (bunc) and severe feather pecking (seve) between the phenotype (homepen behaviour) and the social test without (soc) and with (soc+) a bunch of feathers and the individual test (bold values p<0.05; italic values p<0.10).

Age	Gent Soc	Gent Soc+	Bunc Indiv+	Bunc Soc+	Seve Soc	Seve Soc+
7	0.18	-	-0.05	-	0.00	-
10	0.15	0.12	-0.08	0.03	0.29	0.37
13	0.11	0.07	0.03	0.11	0.11	0.39
16	0.01	-0.06	0.10	0.02	0.26	0.21
19	0.13	-0.03	0.01	0.14	0.00	0.14
22	0.23	0.14	-0.20	-0.17	-0.05	0.18
25	0.22	0.22	0.13	0.24	-0.05	0.15
28	0.09	0.23	-0.11	0.30	-0.05	-0.05
31	0.21	0.25	0.13	0.23	-	-
34	-0.07	0.20	0.13	0.25	0.20	0.20
Chi Square	34.04	32.35	12.70	35.10	27.84	44.25
Comb. P	<0.05	<0.05	>0.05	<0.05	>0.05	<0.05

Over all ages, gentle feather pecking in the homepen corresponded with gentle feather pecking in the social test without a bunch of feathers (Chi Square= 34.04; DF=20; $p<0.05$). Also gentle feather pecking (Chi Square= 32.35; DF=18; $p<0.05$) and bunch pecking (Chi Square= 35.10; DF=18; $p<0.05$) in the social test with a bunch of feathers corresponded with the homepen results over all ages. Bunch pecking in the individual test was not corresponding with gentle feather pecking in the homepen (Chi Square= 12.70; DF=20; $p>0.05$). Severe feather pecking in the homepen corresponded with severe feather pecking in the social test with bunch of feathers over all ages (Chi Square= 44.25; DF=18; $p<0.05$; Table 2.2).

Pecking behaviour in each test was also compared with each bird's genotype (Table 2.3), hypothesising that HFP birds would show more feather and bunch pecking than LFP birds. Over all ages, only severe feather pecking in the social test without a bunch of feathers (Chi Square= 32.36; DF=20; $p<0.05$) and in the social test with a bunch of feathers (Chi Square= 29.93; DF=18; $p<0.05$) showed the expected overall line difference. For gentle feather pecking, HFP birds showed more gentle feather pecking in the social test without bunch at 7 weeks of age. As LFP showed more bunch pecking than HFP birds, most p-values for bunch pecking approach 1 under the hypothesis used, indicating a reverse line difference.

Table 2.3 Simple kappa coefficients of agreement (ranges from -1 to 1) for gentle feather pecking (gent), bunch pecking (bunc) and severe feather pecking (seve) between the between the genotype (HFP or LFP-line) and the social test without (soc) and with (soc+) a bunch of feathers and the individual test (bold values p<0.05; italic values p<0.10).

Age	Gent	Gent	Bunc	Bunc	Seve	Seve
	Soc	Soc+	Indiv+	Soc+	Soc	Soc+
7	0.70	-	-0.07	-	0.03	-
10	0.13	-0.03	-0.27	-0.40	0.07	0.10
13	0.10	-0.07	0.00	-0.17	-0.17	0.03
16	-0.30	-0.47	-0.13	-0.23	-0.13	-0.30
19	-0.20	-0.20	-0.07	-0.23	-0.30	0.03
22	-0.07	-0.10	-0.07	-0.33	0.07	0.20
25	0.03	-0.10	-0.07	-0.13	0.13	0.07
28	-0.13	-0.13	-0.07	-0.20	0.17	0.13
31	-0.10	0.07	-0.07	-0.10	0.13	0.00
34	0.17	-0.03	-0.07	-0.40	0.33	0.27
Chi Square	21.32	12.40	12.61	2.62	32.36	29.93
Comb P	>0.05	>0.05	>0.05	>0.05	<0.05	<0.05

Over all ages, LFP birds performed more ground pecking than HFP birds both in the social test without a bunch of feathers ($F_{1,9}=5.63$; $p<0.05$) and in the homepen ($F_{1,9}=10.30$; $p<0.05$; Figure 2.4); in the social test with a bunch of feathers a tendency was found ($F_{1,8}=4.71$; $p=0.06$). A linear increase of ground pecking over age was found in both the social test with ($F_{1,8}=93.04$; $p<0.001$) and without ($F_{1,9}=72.54$; $p<0.001$) a bunch of feathers.

HFP birds preened more than LFP birds over all ages in the social test with a bunch of feathers ($F_{1,8}=8.71$; $p<0.05$; Figure 2.5) and tended to preen more in the social test without a bunch of feathers

($F_{1,9}$=4.12; p=0.07). An increase in preening behaviour over age was found in both the social test with ($F_{1,8}$=29.42; p<0.001) and without ($F_{1,9}$=120.50; p<0.001) a bunch of feathers.

In the individual test, no line differences were found for percentage of time spent walking over all ages. HFP birds walked more than LFP birds at 7 weeks of age ($F_{1,9}$=7.22; p<0.01) and LFP birds spent more time walking at 16 weeks of age ($F_{1,9}$=14.55; p<0.01; Figure 2.6). HFP birds vocalised more than LFP birds over all ages ($F_{1,9}$=53.69; p<0.001; Figure 2.7). At 7 weeks of age LFP birds vocalised more than HFP birds, but this difference was not significant. From Furthermore, a linear increase in vocalisations over age was found in the HFP line, whereas a decrease was found in the LFP line ($F_{1,9}$=55.50; p<0.001).

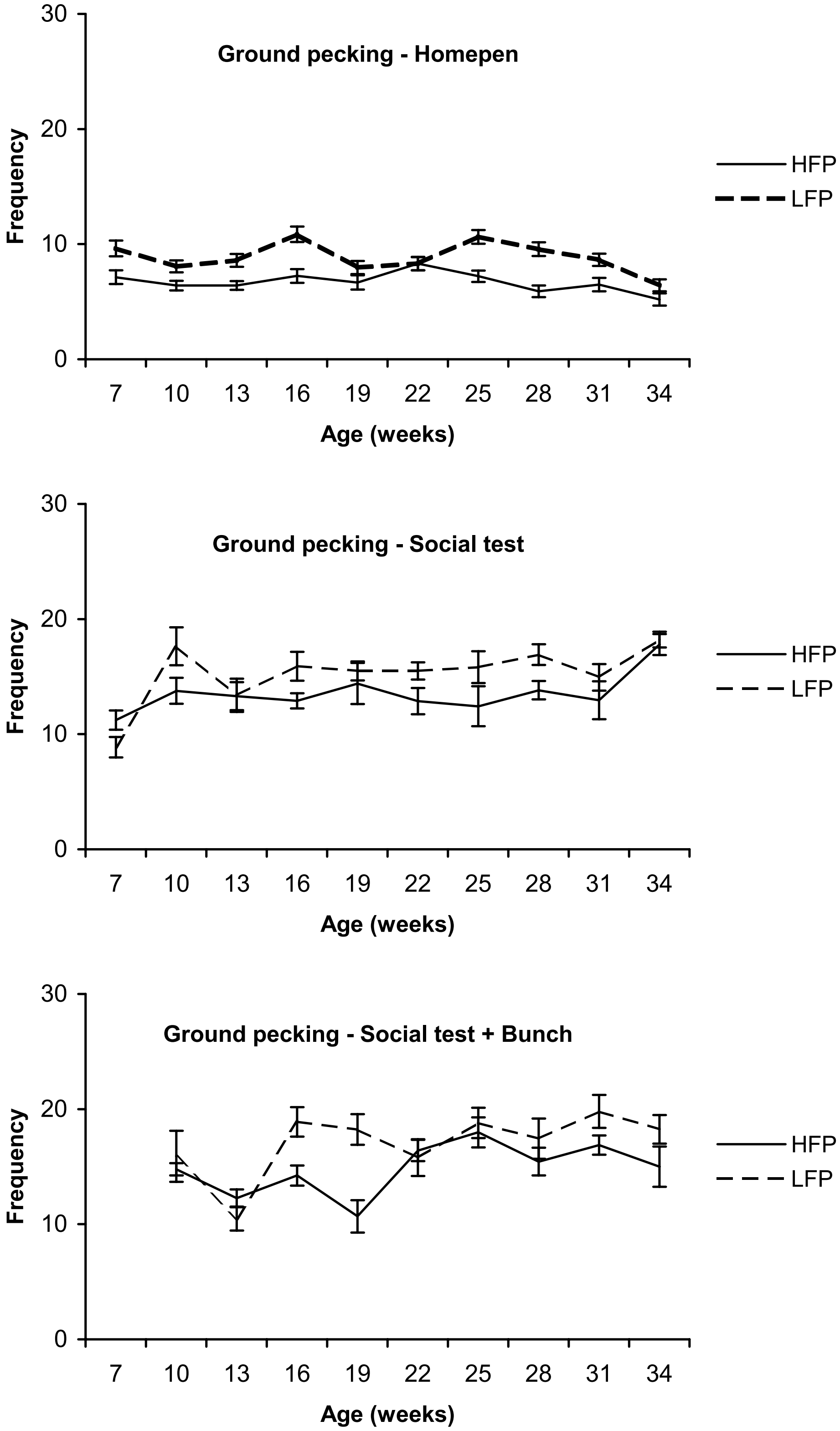

Figure 2.4 Mean number of bouts of ground pecking over time in the homepen (top panel) and in the social tests without- (middle panel) and with (bottom panel) a bunch of feathers in the HFP and LFP lines.

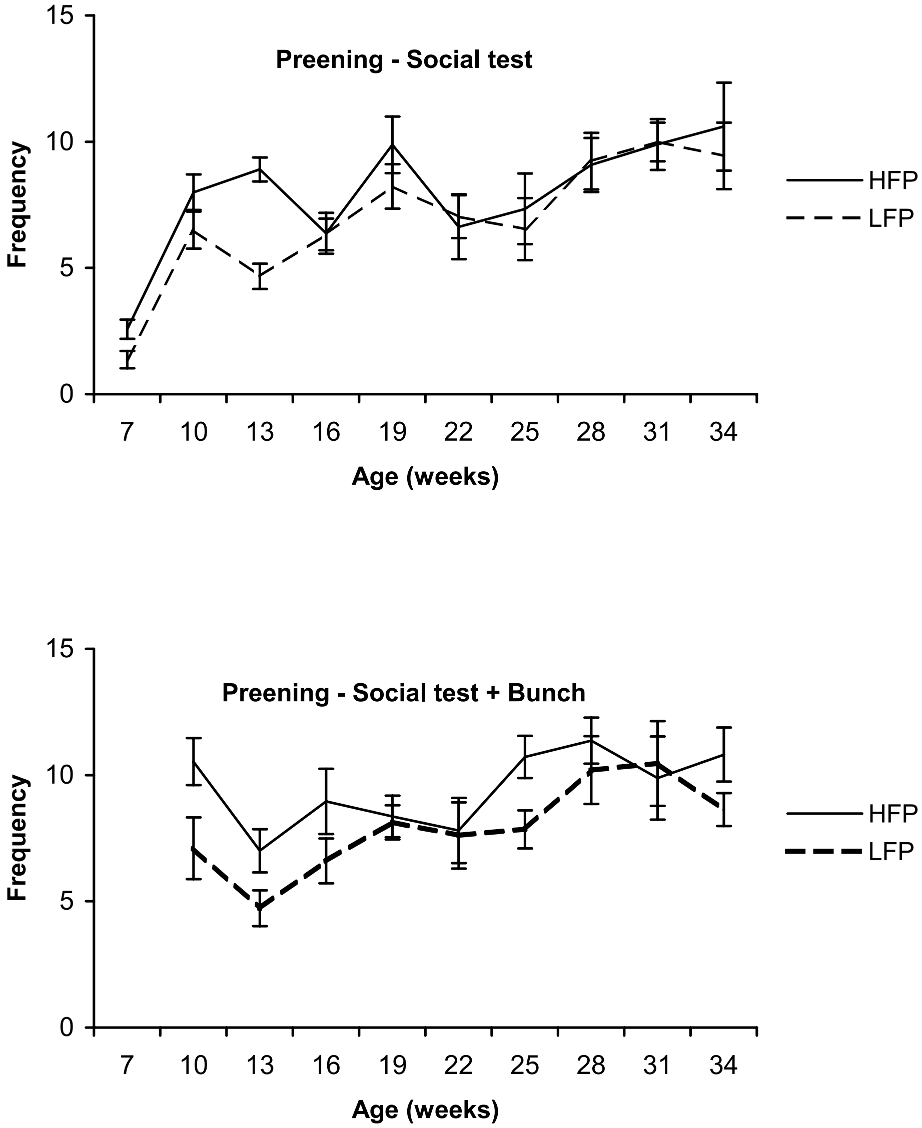

Figure 2.5 Mean number of bouts of preening behaviour over time in the social test without (top panel) and with (bottom panel) a bunch of feathers in the HFP and LFP lines.

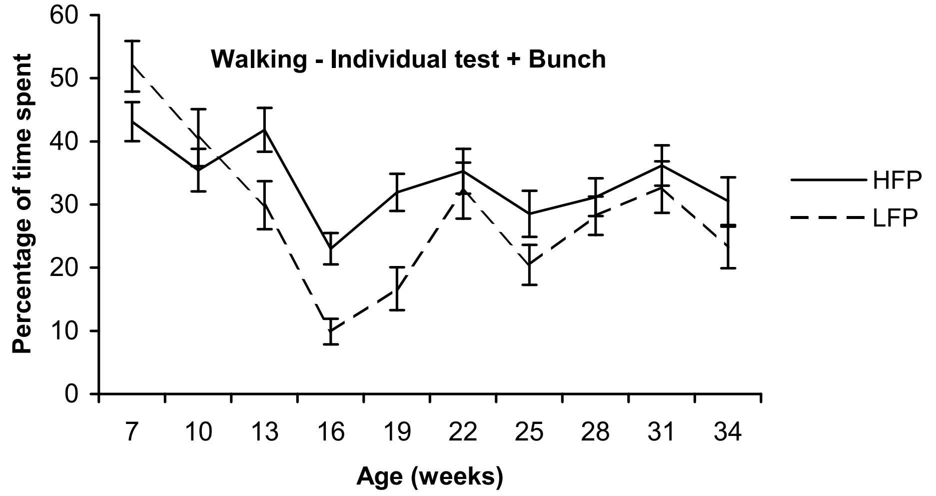

Figure 2.6 Percentage of time spent walking over time in the individual test with a bunch of feathers in the HFP and LFP lines.

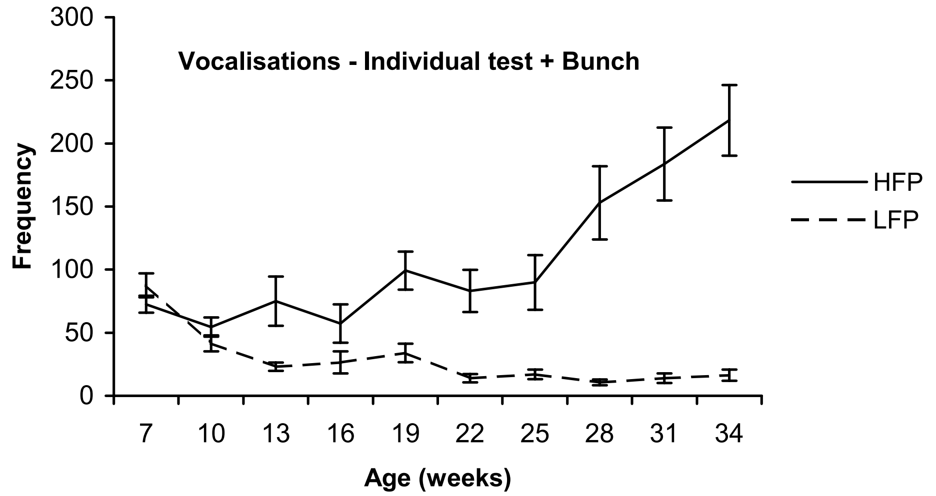

Figure 2.7 Mean number of vocalisations over time in the individual test with a bunch of feathers in the HFP and LFP lines.

Discussion

The aim of the current experiment was to select an appropriate test to measure feather pecking in laying hens. Pecking behaviour in individual and social feather pecking tests was compared with pecking behaviour in the homepen in two lines of laying hens that differed in their propensity to display feather pecking.

In the homepen, HFP birds showed more gentle feather pecking over all ages than LFP birds, as was expected. In the social tests, lines did not differ in gentle feather pecking over all ages. HFP birds showed more severe feather pecking over all ages than LFP birds both in the homepen and the social test without a bunch of feathers. Against our expectations, LFP birds showed more bunch pecking than HFP birds over all ages in the social test with a bunch of feathers and in the individual test.

To a large extent, these results are in line with our hypothesis. Only the fact that LFP birds showed more bunch pecking than HFP birds over all ages was unexpected. These findings are in support of results presented by Cloutier et al. (2000) on pecking at inanimate stimuli as a predictor of cannibalism. They found no correlation between pecking at a bunch of feathers and at flock mates. A tendency was found for future cannibals to have a longer latency to peck the inanimate stimuli (Cloutier et al., 2000). It may well be that the same applies to HFP birds. In an experiment in which the feather pecking test, as described by Bessei et al. (1997) was used and in which the same lines were used as in the present experiment, results were similar to the present study (Van Hierden et al., 2000).

To validate these tests, pecking behaviour in each test was compared with each bird's phenotypic (homepen behaviour) and genetic (line) information. We found that there was correspondence between gentle feather pecking in the homepen and gentle feather pecking and bunch pecking in the social test. Bunch pecking in the individual test was not a reliable measure of gentle feather pecking in the homepen. The presence of absence of conspecifics seems to influence bunch pecking behaviour. For severe feather pecking, correspondence between homepen and the social test with a bunch of feathers was also found. Comparing each bird's line with its pecking behaviour in the tests, we found that severe feather pecking showed the expected line differences over all ages in both social tests. For gentle feather pecking, the expected line difference was only found at 7 weeks of age in the social test without a bunch of feathers. The line difference in bunch pecking was opposite from our hypothesis.

In general, the levels of feather pecking and the development of feather pecking over time were comparable between the homepen and the social tests. In both test environments, gentle feather pecking decreased and severe feather pecking increased over time. This is in agreement with the theory presented by McAdie and Keeling (2002), that gentle feather pecking may develop into severe feather pecking. The fact that LFP birds showed more ground pecking than HFP birds supports the theory of Blokhuis (1986), that feather pecking is redirected ground pecking.

We hypothesised that differences in pecking behaviour would be consistent in the homepen and in the different feather pecking tests and that the testing environment would not have major effects on the behaviour of the birds, if birds were not isolated from their group. The results of the social tests show that birds are ground pecking and preening from 7 weeks onwards at levels comparable with the homepen. Both ground pecking and preening showed an increase over age in the social tests, which may be a sign of habituation to the tests.

In the individual test, HFP birds showed an increase in vocalisations over time, whereas LFP birds showed a decrease. This difference became apparent from 16 weeks of age onwards. Jones et al. (1995) found that LFP chicks uttered more distress calls than HFP chicks in an open-field test at young age, suggesting they have a higher social motivation. In quail, however, birds selected for high social motivation showed more feather pecking (Bilcík and Bessei, 1993), although feather pecking in quail is related with aggression (Wechsler and Schmid, 1998) and not with redirected foraging as in laying hens (Blokhuis, 1986). As vocalisations change from mainly distress calls to mainly alarm calls between 13 and 16 weeks of age (Rodenburg, pers.com.), the large difference between the lines is found in alarm calls and not so much in the distress calls. HFP and LFP lines seemed to have different ways of reacting to the repeated testing procedure. LFP birds seem to habituate to the test procedure, whereas HFP do not seem to habituate. These differences may be caused by different underlying coping strategies. Korte et al. (1997) showed that

LFP birds have a stronger stress response to a manual restraint test, resulting in higher levels of plasma corticosterone after restraint. They suggested that LFP birds are reactive copers (conservation-withdrawal response) whereas HFP birds are proactive copers (fight-flight response). As reactive copers may habituate sooner to a novel environment (Koolhaas et al., 1999), our results support the suggestion from Korte et al. (1997).
Furthermore, HFP birds performed more feather pecking and more feather preening than LFP birds in this experiment, whereas LFP birds showed more bunch pecking and ground pecking. This is in line with the results found by Van Hierden et al. (2002) in younger HFP and LFP birds and indicates that these lines have different substrate preferences for pecking behaviour. HFP birds seem to be more animal directed and LFP birds more environment directed. This is also in agreement with the findings of Johnsen and Vestergaard (1996), who showed that LFP chicks preferred sand for dustbathing, where HFP birds preferred feathers. Furthermore, LFP birds showed more severe feather pecking than HFP birds when housed in cages (McAdie and Keeling, 2002). This indicates that when no substrate for pecking is available, both lines will develop severe feather pecking. When birds have a choice, however, HFP birds seem to prefer feathers to peck at, whereas LFP birds peck more at their environment.

In general, HFP birds showed more gentle and severe feather pecking than LFP birds, whereas LFP birds showed more ground pecking and, unexpectedly, more bunch pecking. Birds that showed gentle feather pecking in the homepen also showed gentle feather pecking and bunch pecking in the social test over all ages. Severe feather pecking in the social test with a bunch of feathers was a good measure of severe feather pecking in the homepen. Bunch pecking in the individual test, however, was not a reliable measure for feather pecking in this experiment. Underlying differences in behavioural strategies, expressed in the behavioural response to the individual test and in different substrate preferences between the lines may have influenced pecking behaviour. In conclusion, gentle and severe feather pecking and bunch pecking in the social test corresponded best with homepen behaviour, whereas bunch pecking in the individual test did not.

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Chapter 3
Reaction to frustration in high and low feather pecking laying hens

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Abstract

Reaction to frustration of high (HFP) and low (LFP) feather pecking laying hens was investigated. From a HFP-line and a LFP-line five birds with a HFP- and five birds with a LFP-phenotype were selected. Birds from the HFP-line were expected to show more key pecking and covered feeder pecking during frustration than birds from the LFP-line. When a bunch of feathers was presented, birds with a HFP-phenotype were expected to redirect their pecks at the bunch. Birds were trained to peck a key for a food reward in an automated Skinnerbox and subjected to two sessions: a control session, where food was available, and a frustration session, where the feeder was covered with Perspex. These two sessions were repeated in the presence of a bunch of feathers. Unexpectedly, birds from the LFP-line had a stronger reaction to frustration than birds from the HFP-line, expressed in pecking behaviour. When a bunch of feathers was offered, birds with a HFP-phenotype did not show more bunch pecking during frustration than birds with a LFP-phenotype.

Introduction

Feather pecking behaviour in laying hens is characterised by non-aggressive pecks at plumage of other birds. Feather pecking varies from gentle, non-damaging pecks to severe feather pecks and pulls. Severe feather pecking results in denuded areas and wounds on the victims body and may lead to tissue pecking and cannibalism (Savory, 1995). One of the main theories on the causation of feather pecking stated that feather pecking is redirected ground pecking (Blokhuis, 1986). Laying hens that lacked proper floor substrate during rearing showed more feather pecking than birds that did have floor substrate during rearing, even when both groups were supplied with floor substrate after rearing (Blokhuis, 1986).

Frustration may play a role in the development of feather pecking. Frustration of feeding behaviour, for instance, can induce pecking behaviour in laying hens. Duncan and Wood-Gush (1972) observed high levels of pecking at the cover and at other parts of the cage, when a covered food reward was offered. Lindberg and Nicol (1994) performed an experiment in which they tried to reduce feather pecking by supplying birds with operant feeders. The idea was that the birds would direct more pecks at the devices and less at other birds. As a result, birds with operant feeders surprisingly developed more feather pecking than birds with normal feeders. They proposed a model in which frustration, for instance because a bird tries to reach the operant feeder but is unsuccessful, results in increased arousal, aggression and fear. Under these circumstances, occasional pecks at the plumage of other birds may develop into more damaging forms of feather pecking (Lindberg and Nicol, 1994). Not only the lack of pecking substrate affects pecking behaviour. Seeing litter but not being able to peck at it, for instance, resulted in higher levels of pecking at a bunch of feathers compared with the absence of litter (Kim-Madslien and Nicol, 2001).

The high (HFP) and low (LFP) feather pecking lines, used for this experiment, were used in previous studies (Johnsen and Vestergaard, 1996; Korte et al., 1997). HFP chicks showed more feather pecking than LFP chicks and dustbathed less on sand, when both lines were trained to dustbathe on a skin of feathers and then given the choice between sand and feathers. HFP chicks seemed to perceive feathers as substrate fit for dustbathing, resulting in reduced dustbathing performance in later life and increased feather pecking. This perception may be caused by a developmental defect (Johnsen and Vestergaard, 1996). LFP birds showed a stronger corticosterone response to manual restraint than HFP birds. It was suggested that these line differences may be caused by underlying differences in coping strategy (Korte et al., 1997). Coping strategy is defined as a coherent set of behavioural and physiological measures. The pro-active coping strategy is characterised by an active behavioural response (fight/flight) and inflexibility in behavioural response towards changes in the environment. The reactive coping strategy is characterised by a passive behavioural response (conservation / withdrawal) and high reactivity to the environment (Koolhaas et al., 1999). Birds from the HFP-line may be characterised as pro-active copers and birds from the LFP-line as reactive copers (Korte et al., 1997).

The objective of the current experiment was to investigate reaction to frustration in high (HFP) and low (LFP) feather pecking laying hens, both genetically (in a high and a low feather pecking line) and phenotypically (in birds from these lines that showed high or low levels of feather pecking, when housed in a group). Two experiments were conducted in a Skinnerbox: in experiment 1 the reaction to frustration was studied; in experiment 2 a bunch of feathers was offered to study substrate preference for redirected pecking. In experiment 1, it was hypothesised that, during frustration, birds from the HFP-line would be more persistent in key pecking and covered feeder pecking than birds from the LFP-line, reflecting a pro-active, less flexible coping strategy. Birds with a HFP-phenotype may also show more pecking behaviour during frustration than birds with a LFP-phenotype, if there is a relationship between their propensity to peck feathers and their frustration-induced pecking behaviour. In experiment 2, it was hypothesised that birds with a HFP-phenotype would peck more at this bunch of feathers during the frustration session than birds with a LFP-phenotype, in accordance with the theory of Lindberg and Nicol (1994). Birds with a LFP-phenotype may redirect their pecks at the floor and the walls of the Skinnerbox.

Materials and methods

Animals and housing

Two lines of laying hens were used for the experiment: the high (HFP) and the low (LFP) feather pecking lines. These lines have been selected for productive traits and show a consistent difference in propensity to develop feather pecking as well. Previous to experiments 1 and 2, the birds were housed from 20 weeks of age in six groups of ten birds: two groups of birds from the HFP-line, two groups of birds from the LFP-line and two mixed groups. The birds were housed in pens measuring 1.5 x 1.5 m, on wooden slats with ad libitum food and water, two laying nests and a perch. Pecking behaviour in the homepen was studied from 22 weeks of age during four consecutive weeks, observing gentle and severe feather pecking, aggressive pecking, food and ground pecking. Ten birds per line were selected for the experiment, based on severe feather pecking behaviour in the group: 5 birds with a HFP- and 5 birds with a LFP-phenotype of each line (Table 3.1). Birds from each of the six groups were selected.

Table 3.1 Mean frequency of bouts of gentle and severe feather pecking per 30 minutes in high (HH) and low (HL) feather peckers from the HFP-line and high (LH) and low (LL) feather peckers from the LFP-line.

Group	N	Line	Pheno	Gentle	Severe
HH	5	H	H	3.43	4.62
HL	5	H	L	0.48	0
LH	5	L	H	1.84	5.60
LL	5	L	L	0.35	0

Birds were re-housed in individual cages (see below) at 35 weeks of age. Training started at 40 weeks of age. Experiment 1 was performed 14 weeks after the first training and experiment 2 was conducted 12 weeks after experiment 1. Training was stretched over a long period because the available training time per week was limited. Cages of the type described by Van Liere and Wiepkema (1992) were used, measuring 100 x 50 x 50 cm (l x w x h). Each cage was equipped with a dustbath and a nestbox and had a partly slatted floor. Food and water were available ad libitum. Lights were on from 3:00 until 19:00. The Wageningen University Committee on Animal Care and Use has approved this experiment.

Apparatus

Four automated Skinnerboxes were located in a sound attenuated room, close to the homecages. Each Skinnerbox measured 60 x 50 x 65 cm. Three lighted keys were present 10 cm apart on the intelligence panel, 26 cm above the floor. The feeder was accessible through a round hole (12 cm in diameter) in the centre of the intelligence panel, 10 cm above the floor. Food was only accessible when the feeder was up. The presence or absence of a bird's head in the feeder was detected by a photocell. A 5-W house-light was fixed 8 cm above each Skinnerbox. The Skinnerboxes were operated through a custom-made program, using LabView® software (National Instruments, 1994). Changes in key lights (on or off), keys (peck or no peck) and photocells (head or no head) were automatically recorded and stored on disk. Skinnerbox and computer were located in the same room. For the training sessions, two Skinnerboxes were used. For the experimental sessions, only one box was used to avoid interference.

Procedure experiment 1

Each bird was habituated to a Skinnerbox for ten minutes on the first day of training. On the following days, birds were food deprived for five hours and each bird was hand-shaped daily in a 10-min shaping session to press one of the three keys for a food reward. During shaping all keys were illuminated continuously and the house-light was on. A 5-sec food reward was given manually by the observer, by pressing a key on the computer. Birds were shaped by allowing them to eat 5 sec after they had pressed a key. When all birds were able to peck a key for a food reward, each bird was food deprived for 24 hours and operant training was used to train each bird to peck a key when the stimulus lights were on. They were trained for 15 min per day. At the start of each session the house-light was switched on. After a variable interval (30 ± 2 sec) the keys were illuminated and a 10-sec interval started in which a key peck was rewarded with a 5-sec food reward. Immediately after the bird had pressed a key, the key lights were switched off and the feeder came up. After 5 sec the feeder went down and the next variable interval started. Each bird was trained until the training criterion was reached: at least 90% correct key pecks and head in feeder within 3 sec after the feeder came up. Sixteen birds, four per line/phenotype combination, reached the training criterion. After 24 hours food-deprivation, each bird was subjected to two 15-min test sessions on two consecutive days: a control session, in which the feeder was normally accessible and a frustration session, in which the feeder was covered with Perspex. Sessions were conducted between 10:00 and 16:00 to avoid interference with egg laying. Behaviour and vocalisations were recorded on videotape using a video-camera connected to a video-recorder and an external microphone, placed on top of the Skinnerbox and directly plugged into the video-recorder. Behaviour was analysed from videotape with The Observer® programme (Noldus, 1993) using focal sampling. The ethogram focused on pecking behaviour, locomotion and vocalisations and is described in Table 3.2.

Table 3.2 Ethogram used for the behavioural observations.

Behaviour	Definition
Key peck	Peck at one of the keys
Covered feeder peck[1]	Peck at the covered feeder
Eating bout[2]	Bout of pecking in the feeder
Wall peck	Peck at the wall or on the ceiling
Ground peck	Peck at the ground
Microphone peck	Peck at the microphone
Bunch peck[3]	Peck at the bunch of feathers
Preening bout	Bout of preening feathers or legs
Pacing bout	Bout of walking to and fro
Standing bout	Bout of standing inactive
Walking bout	Bout of walking (min. 2 steps)
Sitting bout	Bout of sitting
Gakel call	Gakel call: [Pwoook pwok pwok]
Alarm call	Alarm call: [Kot kot kot kodeeek]

[1]Only possible during the frustration session
[2]Only possible during the control session
[3]Only possible in experiment 2

Birds were tested using an alternating schedule for the four experimental groups. Order of testing was kept the same during the control and the frustration session.

Procedure experiment 2

Twelve weeks after experiment 1 another experiment was conducted with the same 16 birds. Each bird was food deprived for 24 hours and retrained for 15 min in the presence of a bunch of white tail feathers, placed opposite to the intelligence panel, close to the Perspex front. During this training, each bird was required to reach the training criterion set in experiment 1. After retraining, birds were subjected to a control session and a frustration session identical to the sessions described before; the only difference being the presence of the bunch of feathers. The same ethogram was used for the behavioural observations, only pecking at the bunch of feathers was added to the original ethogram (see Table 3.2).

Analysis

All pecks, except for pecks at the keys, at the food and at the covered feeder, were summed as a measure for redirected pecking. Two-tailed analysis of variance was performed using the GLM-procedure in the SAS® statistical programme (SAS, 1996). Frequencies of all observed behaviours were transformed with a square root transformation, because data were not distributed normally. Testing order, order of treatment and pen (in the previous experiment) were included in the original model as fixed effects, but only testing order had an effect. The final model for analysis included the fixed effects line, phenotype, and testing order. Also the interaction between line and phenotype was calculated. Repeated measures analysis of variance was used to compare the frustration session to the control session. To study the effect of frustration on key pecking over time, the session was divided in five periods of three minutes and analysed using orthogonal polynomial contrasts (Sokal and Rohlf, 1969, pages 470-475).

Results

Experiment 1

During the first three minutes of the frustration session an increase in key pecking was found compared with the control session ($F_{1,9}=16.38$; $p<0.01$), followed by a linear decrease over time ($F_{1,9}=48.47$; $p<0.001$; Figure 3.1).

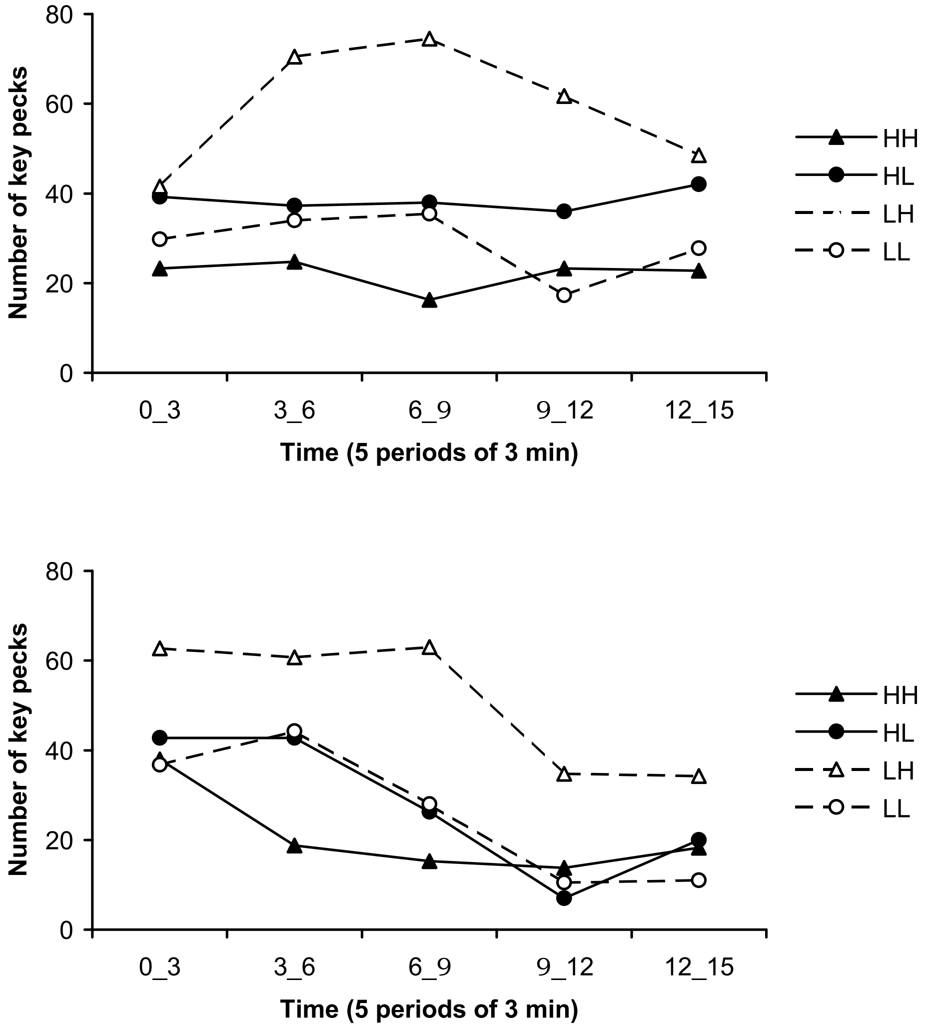

Figure 3.1 Mean number of key pecks during control (top panel) and frustration (bottom panel) over five periods of three minutes in high (HH) and low (HL) feather peckers from the HFP-line and high (LH) and low (LL) feather peckers from the LFP-line.

Birds from the LFP-line pecked more at the keys than birds from the HFP-line within the frustration session ($F_{1,9}$=6.13; p<0.05) and tended to peck more at the keys as an effect of frustration ($F_{1,9}$=4.95; p=0.05). No effect of phenotype was found on key pecking. A tendency was found for the interaction between line and phenotype ($F_{1,9}$=3.64; p=0.09). Birds from the LFP-line with a HFP-phenotype tended to peck more at the keys than the other groups (Figure 3.1).

Birds from the LFP-line pecked more at the covered feeder than birds from the HFP-line as an effect of frustration ($F_{1,9}$=15.85; p<0.01). A tendency was found for birds with a HFP-phenotype to peck more at the covered feeder than birds with an LFP-phenotype ($F_{1,9}$=4.68; p=0.06).The total number of redirected pecks increased as an effect of frustration over all experimental groups ($F_{1,9}$=37.06; p<0.001). Birds with a LFP-phenotype tended to show more redirected pecking than birds with a HFP-phenotype ($F_{1,9}$=5.10; p=0.05) as an effect of frustration (Figure 3.2). No effect was found for the interaction between line and phenotype for both covered feeder pecking and redirected pecking.

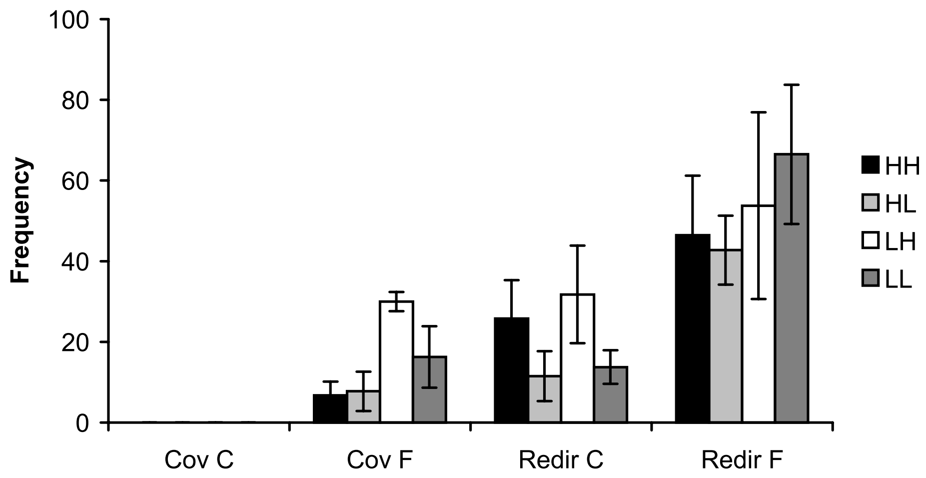

Figure 3.2 Mean frequencies of covered feeder pecks (cov) and redirected pecks (redir) during control (C) and frustration (F) in high (HH) and low (HL) feather peckers from the HFP-line and high (LH) and low (LL) feather peckers from the LFP-line.

Experiment 2

Birds from the LFP-line again pecked more at the covered feeder than birds from the HFP-line ($F_{1,9}$=11.20; p<0.01) when the frustration session was compared with the control session. Birds with a HFP-phenotype tended to peck more at the covered feeder than birds with a LFP-phenotype ($F_{1,9}$=3.55; p=0.09). No interaction effects were found.

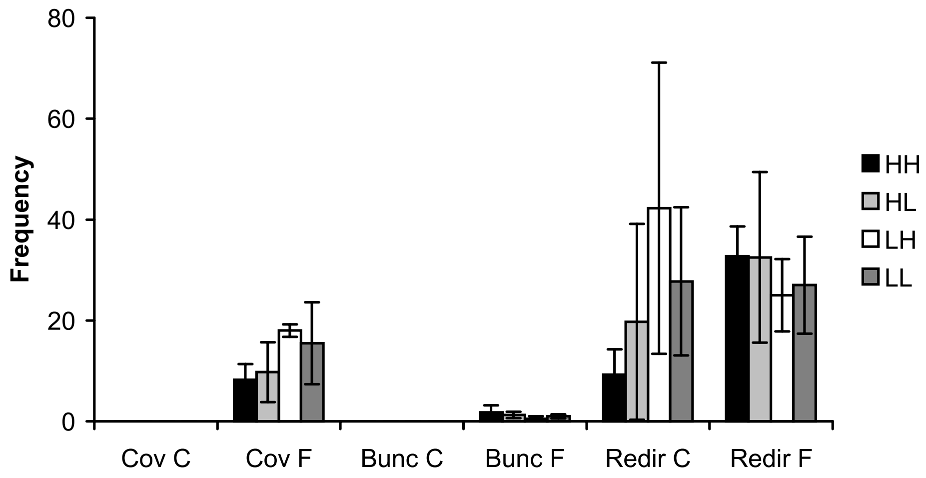

Figure 3.3 Mean frequencies of covered feeder pecks (cov), bunch pecks (bunc) and redirected pecks (redir) during control (C) and frustration (F) in high (HH) and low (HL) feather peckers from the HFP-line and high (LH) and low (LL) feather peckers from the LFP-line.

Overall, birds performed more bunch pecking as an effect of frustration ($F_{1,9}$=11.39; p<0.01). Bunch pecking was only observed during the frustration session. Levels of bunch pecking were low. No effect of line or phenotype was found. Birds did not show more redirected pecking as an effect of frustration, in contrast with experiment 1 (Figure 3.3). Birds showed less redirected pecking during frustration compared with experiment 1 (mean 30.4 ± 4.9 pecks vs. 52.4 ± 7.8 pecks). Again, birds from the LFP-line pecked more at the keys than birds from the HFP-line within the frustration session ($F_{1,9}$=6.02; p<0.05). No phenotype or interaction effects were found for key pecking.

Discussion

The objective of the current experiment was to investigate reaction to frustration in high (HFP) and low (LFP) feather pecking laying hens, both genetically (in a high and a low feather pecking line) and phenotypically (in actual high and low feather peckers within the two lines). It was hypothesised that, during frustration in experiment 1, birds from the HFP-line would be more persistent in key pecking and covered feeder pecking than birds from the LFP-line. Birds with a HFP-phenotype may also show more pecking behaviour during frustration than birds with a LFP-phenotype, if there is a relationship between their propensity to peck feathers and their frustration-induced pecking behaviour. In experiment 2 a bunch of feathers was presented during testing. It was hypothesised that birds with a HFP-phenotype would peck more at this bunch of feathers during the frustration session than birds with a LFP-phenotype.

Unexpectedly, birds from the LFP-line pecked more at the keys within the frustration session than birds from the HFP-line. No evidence was found that birds from the HFP-line were more persistent in their pecking behaviour, reflecting a pro-active coping strategy. Birds from the LFP-line also pecked more at the covered feeder than birds from the HFP-line as an effect of frustration. No effect of line was found in number of food pecking bouts during control, suggesting that the difference in pecking at the covered feeder during frustration is not caused by differences in pecking at the feeder per se. No line differences were found in redirected pecking. Birds from the LFP-line seem to be more persistent in their attempts to reach the covered food reward and may have a stronger reaction to frustration, which was against our expectations.

For the effects of phenotype on pecking behaviour only tendencies were found. Birds from the LFP-line with a HFP-phenotype tended to peck more at the keys than the other groups, indicating a relationship between key pecking during frustration and feather pecking within the LFP-line. Birds with a HFP-phenotype tended to be more persistent in pecking at the covered feeder than birds with a LFP-phenotype as an effect of frustration, whereas birds with a LFP-phenotype tended to show more redirected pecking to other parts of the Skinnerbox.

For experiment 2, we hypothesised that, based on the theory of Blokhuis (1986), birds with a HFP-phenotype would be more likely to redirect their pecking behaviour to feathers, if available. Overall, birds performed more bunch pecking as an effect of frustration in experiment 2. Bunch pecking was only observed during the frustration session. Levels of bunch pecking were low compared with other experiments where a bunch of feathers was used (Bessei et al., 1997; Kim-Madslien and Nicol, 2001). No effect of phenotype or line was found. The low levels of bunch pecking might be caused by the location of the bunch of feathers. Birds were focused on the intelligence panel, especially during the control session, although they moved around frequently during the frustration session. When they were standing in front of the keys, the bunch of feathers was located behind them. Another explanation might be that the bunch of feathers is not particularly attractive to redirect pecking at and that this is not a very suitable model for feather pecking. The fact that birds of both phenotypes pecked at the bunch of feathers indicates that the bunch of feathers is perceived as just another substrate for redirected pecking, and not as a specific substrate for feather pecking. Perhaps the feathers should be presented in a different manner, baring more resemblance with a real bird. Jones (2001), however, showed that movement does not make pecking devices more attractive to birds. Haskell et al. (2000) performed a runway-experiment in which a dominant bird was frustrated in the presence of a sub-dominant bird. In accordance with their hypothesis, aggressive interactions increased as a result of frustration, but also more feather pecking was observed during frustration (Haskell et al., 2000). These results support the hypothesis that feather pecking can be triggered by frustration in the presence of another bird.

In experiment 2, birds from the LFP-line again pecked more at the covered feeder and at the keys than birds from the HFP-line as an effect of frustration. Birds did not show more redirected pecking as an effect of frustration and pecked less to the environment compared with experiment 1. This difference in redirected pecking behaviour between the two experiments may have been caused by habituation to the frustration session or by the difference in age of the birds (12 weeks). Birds with a HFP-phenotype tended to peck more at the covered feeder than birds with a LFP-phenotype, consistent with the results found in experiment 1.

In these experiments, differences were found in reaction to frustration between high and low feather peckers, both genetically and phenotypically. Opposite to our hypothesis, birds from the LFP-line had a stronger reaction to frustration than birds from the HFP-line, expressed in key pecking and covered feeder pecking. Birds with a HFP-phenotype tended to peck more at the covered feeder than birds with a LFP-phenotype, whereas these birds tended to show more redirected pecking as an effect of frustration. When a bunch of feathers was offered, no effects on bunch pecking of line or phenotype were found. Birds with a HFP-phenotype showed much feather pecking in the social context of their original groups (Table 3.1), but did not perform more bunch pecking than birds with an LFP-phenotype during frustration in the non-social context of experiment 2.

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Chapter 4
Reaction to frustration in high and low feather pecking lines of laying hens from commercial or semi-natural rearing conditions

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Submitted

Abstract

The effect of rearing conditions on feather pecking and reaction to frustration was studied in two lines of laying hens. From commercial rearing conditions (large group, no mother hen), seven birds from a high feather pecking line (HC birds) and eight birds from a low feather pecking line (LC birds) were used. From semi-natural rearing conditions (small group, mother hen present) seven birds from the high feather pecking line (HN birds) were used.

Feather pecking behaviour of HC, LC, and HN groups was recorded for 30 minutes. After that, each bird was food deprived and trained to peck a key for a food reward in a Skinnerbox. After training, each bird was subjected to a frustration session in a Skinnerbox, where the feeder was covered with Perspex.

Three HC birds showed severe feather pecking, compared with one HN bird and zero LC birds. Differences in reaction to frustration were found between birds from different lines, but not in birds from different rearing conditions. LC birds tended to put their head in the feeder more frequently than HC birds over all sessions. Although limited, this study indicates that rearing conditions influence feather pecking, but not reaction to frustration.

Introduction

Feather pecking, i.e. the damaging and removal of feathers, is a common problem in laying hens (Blokhuis and Wiepkema, 1998). In modern poultry husbandry, chicks are hatched in brooders and reared in large groups without a mother. Both the absence of a mother and the large group size, as opposed to the natural group size, may be associated with the development of feather pecking behaviour. Larger groups in general showed more feather pecking than smaller groups, both in experiments with chicks (Savory et al., 1999) and with adult laying hens (Allen and Perry, 1975; Bilcík and Keeling, 2000).

The presence of a hen during the rearing period has been shown to increase activity of the chicks (Roden and Wechsler, 1998) and influence their food preferences (Wauters et al., 2002) and the emotional and social reactivity of the chicks (Perre et al., 2002). Chicks reared with a hen were less afraid to approach a novel object and had a higher social motivation later in life than chicks reared without a hen (Perre et al., 2002). As feather peckers have been found to be more fearful (Vestergaard et al., 1993) and to have a lower social motivation (Jones et al., 1995) than non-feather peckers, it may be expected that chicks reared with a hen would show less feather pecking at a later age. Chicks reared with a hen followed food preferences expressed by the hen and showed more foraging than chicks reared without a hen (Wauters et al., 2002). As feather pecking has been described as redirected foraging behaviour (Blokhuis, 1986; Huber Eicher and Wechsler, 1997), chicks reared with a hen may be less likely to develop feather pecking. Roden and Wechsler (1998), however, were unable to find differences in feather pecking between groups of chicks with and without a hen, while feather pecking was observed from the first week of life onwards in both conditions.

Riedstra and Groothuis (2002) studied feather pecking behaviour in young chicks from two lines that differed in their propensity to develop feather pecking: the so-called high (HFP) and low (LFP) feather pecking lines. They found a line difference in gentle feather pecking from three days of age onwards. Development of feather pecking was studied in these lines from 0 through 8 weeks of age (Van Hierden et al., 2002) and from 7 through 34 weeks of age (Rodenburg and Koene, 2001). In these studies, the HFP line showed more feather pecking and preening than the LFP line, whereas the LFP line showed more ground pecking and food pecking. HFP and LFP birds seem to have different ways of targeting pecking behaviour. HFP birds may be more animal-directed in their pecking behaviour and LFP-birds more environment-directed (Rodenburg and Koene, 2001; Van Hierden et al., 2002).

Frustration, i.e. the omission of an expected reward, may influence development and targeting of pecking behaviour. Duncan and Wood-Gush (1972) showed that frustration of feeding behaviour induces both pecking behaviour at the covered food reward and redirected pecking at other parts of the cage. Lindberg and Nicol (1994) found that supplying hens with operant feeders resulted in high levels of feather pecking. They proposed a model in which frustration results in increased arousal, aggression, and fear. Under these circumstances, occasional pecks at the plumage of other birds may develop into more damaging forms of feather pecking (Lindberg and Nicol, 1994). To test this model, feather peckers and non-feather peckers of the HFP and

LFP lines described before, were studied under conditions of frustration in a Skinnerbox (Rodenburg et al., 2002). It was expected that birds from the HFP line would show a stronger reaction to frustration than birds from the LFP line, as a possible explanation for the line difference in feather pecking behaviour. Surprisingly, LFP birds showed more covered feeder pecking and key pecking as an effect of frustration than HFP birds. It was discussed that HFP birds may have lacked an appropriate substrate to redirect their pecking behaviour at, i.e. feathers or other birds, although no line differences were found in pecking at a bunch of feathers during frustration (Rodenburg et al., 2002). From this experiment we hypothesised that feathers could be made attractive to peck at by presenting them in a different manner, for instance at one of the keys of the Skinnerbox. Furthermore, it seemed very important to see if rearing conditions influence reaction to frustration in a Skinnerbox, as rearing conditions have been shown to have a major influence on behaviour of the birds in later life (Perre et al., 2002).

The aim of this experiment was to study the effect of rearing conditions on feather pecking and reaction to frustration and the relationship between them. A comparison was made between birds from the HFP line from commercial (HC) and semi-natural (HN) rearing conditions and birds from the LFP line from commercial (LC) rearing conditions. HN and LC birds were expected to show less feather pecking than HC birds in a feather pecking test. During frustration, HN birds might show a different reaction to frustration than HC birds, similar to LC birds. When the least attractive key of the Skinnerbox will be covered with feathers, it might attract key pecking behaviour, especially in HC birds.

Materials and methods

Animals and housing

Laying hens from the so-called high (HFP) and low (LFP) feather pecking lines were used for the experiment. The lines used have been selected for productive traits and showed a consistent difference in propensity to develop feather pecking as well (Rodenburg and Koene, 2001; Riedstra and Groothuis, 2002; Van Hierden et al., 2002), although there is still overlap in feather pecking between those lines (McAdie and Keeling, 2002). Birds of both lines were reared in two different rearing conditions: commercial or semi-natural. All birds were hatched and reared at the University of Groningen. Birds from commercial rearing conditions were hatched in a brooder and reared in groups of 45 chicks. Birds from the semi-natural rearing conditions were also hatched in a brooder, but reared by a foster hen in groups of 6 chicks. From 31 weeks of age, all birds were housed in one large group. At 36 weeks of age, birds were transported to the experimental farm in Wageningen. From 36 through 50 weeks of age birds were housed in one group of 30 birds in a pen measuring 5 x 5 m, with wood shavings on the floor, perches, laying nests and water. At 50 weeks of age, birds were moved to the experimental unit. The experiment started at 52 weeks of age and ended at 60 weeks of age.

From the HFP-line, 7 birds from commercial (HC) and 7 birds from semi-natural (HN) rearing conditions were used; from the LFP-line 8 birds from commercial rearing conditions (LC) were available. Birds were housed in cages of the type described by Van Liere and Wiepkema (1992), measuring 100 x 50 x 50 cm (l x w x h). Each cage was equipped with a dustbath and a nestbox and had a partly slatted floor. Food and water were available ad libitum. Lights were on from 3:00 until 19:00. The Wageningen University Committee on Animal Care and Use has approved this experiment.

Procedure feather pecking test

To study these birds' propensity to perform feather pecking, the three groups of HC, HN and LC birds were tested in a social feather pecking test, as used by Rodenburg and Koene (2001). All birds of one group were caught and transported in a plastic crate to a testing pen. The testing pen had solid walls and a Perspex front with wood shavings on the floor and measured 1.25 x 1.25 m. The birds were placed in the testing pen in darkness. Then the light was switched on and the experimenter left the room. From an adjacent room, the experimenter recorded all aggressive pecks, and gentle and severe feather pecks of each bird. Tests were conducted between 14:00 and 16:00.

Apparatus

Three automated Skinnerboxes were used of the type described by Zimmerman and Koene (1998). They were located in a sound attenuated room, close to the homecages. Each Skinnerbox measured 60 x 50 x 65 cm. Three lighted keys were present 10 cm apart on the intelligence panel, 26 cm above the floor. The feeder was accessible through a round hole (12 cm in diameter) in the centre of the intelligence panel, 10 cm above the floor. Food was only accessible when the feeder was up. The presence or absence of a bird's head in the feeder was detected by a photocell. A 5-W house-light was fixed 8 cm above each Skinnerbox. The Skinnerboxes were operated through a custom-made program, using LabView® software (National Instruments, 1994). Changes in key lights (on or off), keys (peck or no peck) and photocells (head or no head) were automatically recorded and stored on disk. Key pecks when the key lights were switched on, and key pecks when the key lights were switched off could be recorded separately in this manner. Skinnerbox and computer were located in the same room.

Training procedure

Each bird was habituated to a Skinnerbox for 15 min on the first day of shaping. On the following days, each bird was food deprived for 6 hours per day in week 1 and for 23 hours per day in week 2 and auto-shaping was used to train the birds to press one of the three keys for a food reward. Body weight was recorded every day to avoid excessive weight loss. During auto-shaping all keys were illuminated every 30 ± 2 s. The keys were illuminated for 10 s and after that, the feeder came up and the bird was allowed to eat for 5 s. This auto-shaping procedure can be used to train birds to peck a key through pairings of illumination of that key with food (Lieberman, 1993, pp. 96-97). When all birds were pecking at the keys during auto-shaping, each bird was again food deprived for 23 hours per day and operant training was used to train each bird to peck a key when the stimulus lights were on. They were trained for 15 min per day. The house-light was switched on at the start of each session. The training sessions were identical to the auto-shaping sessions, the only difference being that birds had to press one of the keys to get a food reward. Each bird was trained until the training criterion was reached: at least 90% correct key pecks and head in feeder within 3 s after the feeder came up.

Procedure experiment 1

On three consecutive days, each bird was food-deprived for 23 hours and then subjected to one of the three 15-min test sessions: a pre-control session, a frustration session and a post-control session. During both control sessions, the feeder was normally accessible. During the frustration session the feeder was covered with Perspex, so the birds could see and smell the food, but were unable to reach it. Sessions were conducted between 10:00 and 16:00 to avoid interference with egg laying, which occurred in general before 10:00. Order of testing was kept the same during the control and the frustration sessions. During testing we alternated between HC birds, LC birds and HN birds to avoid effects of time of testing.

Procedure experiment 2

Individual key preferences of each bird were analysed prior to experiment 2. Each bird was assigned to one of the three groups of birds with similar key preferences. Most birds had preferences for one or two keys. If all three keys were pecked, the key with the lowest mean number of pecks was selected as the least attractive. Eight birds that pecked least at the right key were assigned to Skinnerbox 1, 14 birds that pecked least at the middle key were assigned equally to both Skinnerbox 2 and 3. The three Skinnerboxes were then fitted with 6 white feathers (4 to 6 cm long) around the key which was pecked least. The lighted key was still fully visible. Each bird was again food deprived for 23 hours and subjected to a pre-control session, a frustration session and a post-control session identical to the sessions described before; the only difference being the presence of the feathers.

Analysis

The data of the feather pecking test were not analysed statistically, as each experimental group was tested as a whole and no replicates were available. The Skinnerbox data were analysed in SAS® (SAS, 1996). Number of key pecks and number of times a bird put its head in the feeder were square root transformed because data were not normally distributed. Effects of line (HC vs. LC) and of rearing condition (HC vs. HN) were analysed separately. The final model for analysis included the fixed effects experimental group (HC and HN or LC) and testing order. Analysis of variance was used for the analysis, taking each bird's pre-control-, frustration-, and post-control sessions as repeated measures. To study the effect of frustration on key pecking over time, the session was divided in five periods of three minutes and analysed using orthogonal polynomial contrasts (Sokal and Rohlf, 1995, pp. 674-676).

Results

Feather pecking test

Aggressive pecking was observed in HC and HN groups (Table 4.1). In both cases, five out of seven birds showed aggression. Almost no aggressive pecking was observed in LC birds. For gentle feather pecking, levels were low in all three groups. Three HC birds showed severe feather pecking in the feather pecking test, whereas levels of severe feather pecking were close to zero (HN birds) or zero (LC birds) in the other groups.

Table 4.1 Mean frequency of bouts of aggressive pecking, and gentle and severe feather pecking per 30 minutes in birds from the HFP-line from semi-natural (HN) or commercial (HC) rearing conditions and birds from the LFP-line from commercial rearing conditions (LC); between brackets the number of birds performing this behaviour (N).

Group	N	Line	Rear	Aggr (N)	Gentle (N)	Severe (N)
HC	7	H	C	4.0 (5)	0.4 (2)	1.3 (3)
HN	7	H	N	8.3 (5)	0.4 (3)	0.1 (1)
LC	8	L	C	0.5 (3)	0.6 (4)	0 (0)

Training

The results of the autoshaping sessions are shown in Figure 4.1. Key pecking increased in all groups from day 1 through day 8 ($F_{1,8}$=12.05; p<0.01; Figure 4.1, upper panel). LC birds tended to peck more at the keys than HC birds at day 1 ($F_{1,4}$=7.68; p=0.05), and at day 2 ($F_{1,4}$=5.74; p=0.07). Between HC and HN birds, no differences in key pecking were found. HN birds tended to put their head in the feeder more frequently than HC birds at day 3 ($F_{1,4}$=5.26; p=0.08; Figure 4.1, middle panel). No line differences were found. As a result of switching from classical to operant conditioning at day 5, birds showed a clear drop in number of times they put their head in the feeder.

The success rate (percentage of successful attempts to get the feeder up) was 100% during classical conditioning from day 1 through 4 (Figure 4.1, lower panel). Therefore, results are only shown for day 5 through 8. The success rate improved in all groups from day 5 through 8 ($F_{1,8}$=13.46; p<0.01).

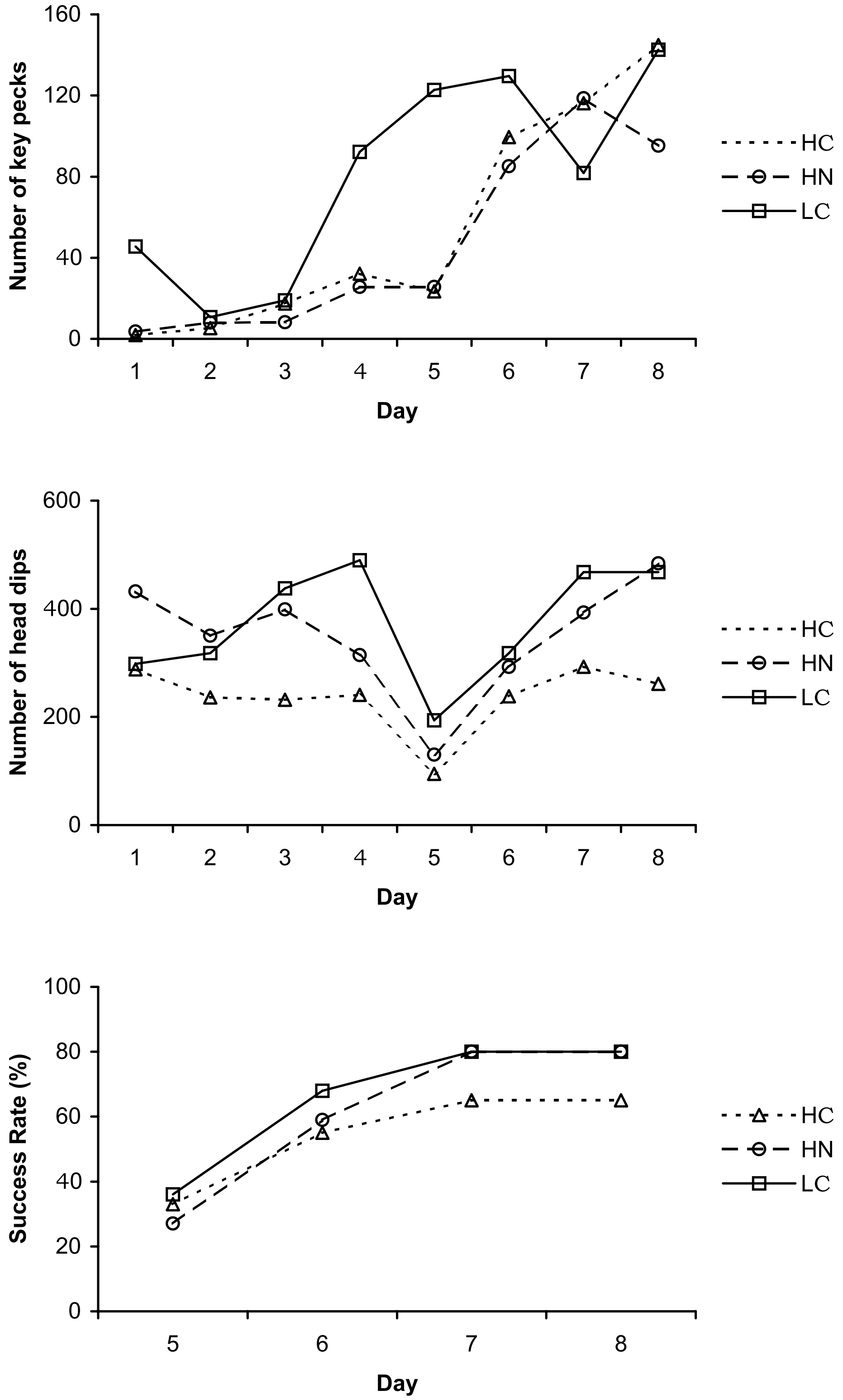

Figure 4.1 The number of key pecks (top panel), the number of head dips in the feeder (middle panel) and the success rate (bottom panel) over time in birds from the HFP line from commercial (HC) and semi-natural (HN) rearing conditions and birds from the LFP line from commercial rearing conditions (LC).

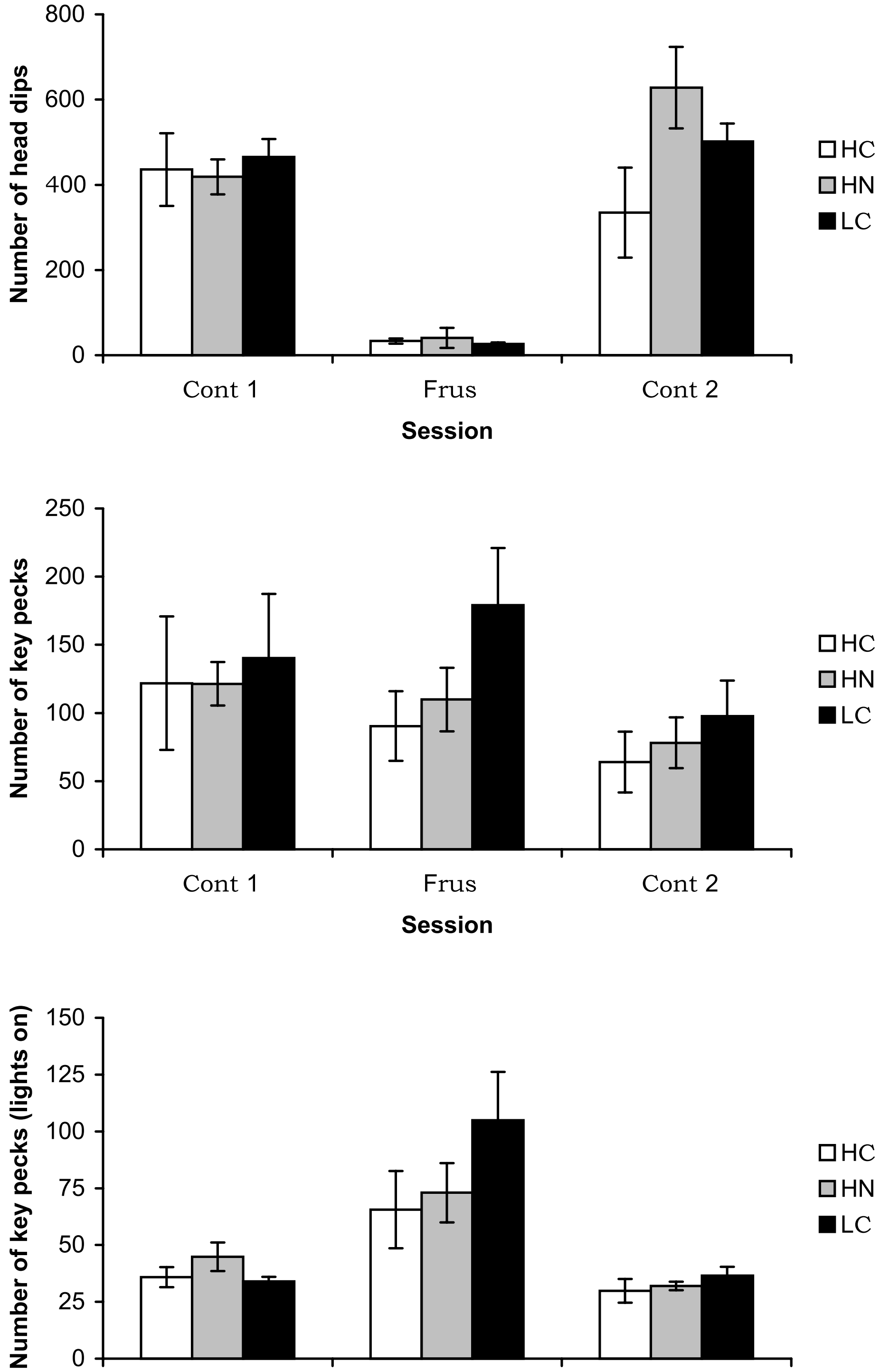

Figure 4.2 The number of head dips in the feeder (top panel), the total number of key pecks (middle panel) and the number of key pecks with key lights 'on' (bottom panel) during pre-control (cont 1), frustration (frus) and post-control (cont 2) sessions in birds from the HFP line from commercial (HC) and semi-natural (HN) rearing conditions and birds from the LFP line from commercial rearing conditions (LC).

Experiment 1

A decrease was found for the frequency birds put their head in the feeder as an effect of frustration (quadratic contrast; $F_{1,12}$=168.06; p<0.001; Figure 4.2, top panel). LC birds tended to put their head more frequently in the feeder than HC birds over all sessions ($F_{1,6}$=4.65; p=0.07). No differences between HC and HN birds were found. There were also no differences between experimental groups in the total number of key pecks during control and frustration sessions (Figure 4.2). When we distinguished between pecks when the key lights were on and pecks when the key lights were off, an increase as a result of frustration was found for key pecking when the key lights were on ($F_{1,12}$= 16.44; p<0.01). Pecking when the key lights were off showed a linear decrease over the three sessions ($F_{1,12}$= 8.92; p<0.05).
When the total number of key pecks during frustration was analysed over five periods of three minutes, a linear decrease over time was found ($F_{1,12}$= 5.04; p<0.05) in the frustration session (Figure 4.3), compared with both control sessions. No differences were found between birds from different lines or rearing conditions.

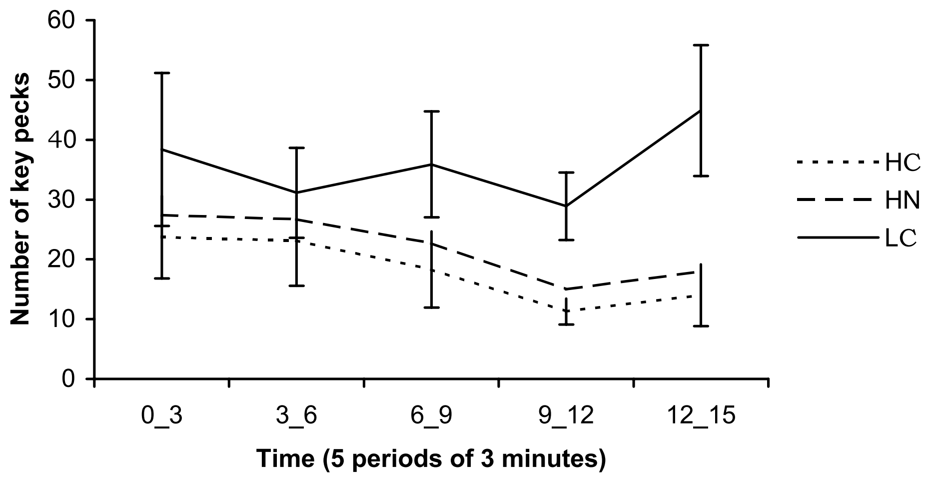

Figure 4.3 Total number of key pecks in 5 periods of 3 minutes during the frustration session in birds from the HFP line from commercial (HC) and semi-natural (HN) rearing conditions and birds from the LFP line from commercial rearing conditions (LC).

Experiment 2

The results for key pecking in experiment 2 were similar to the results found in experiment 1 (Figure 4.3). Overall, birds had lower success rates during the frustration session, compared with both control sessions ($F_{1,12}$=23.27; p<0.001). HN birds tended to have a lower success rate (getting the covered feeder up) than HC birds during the frustration sessions ($F_{1,5}$=5.71; p=0.06). No difference was found between HC and LC birds (Figure 4.4).

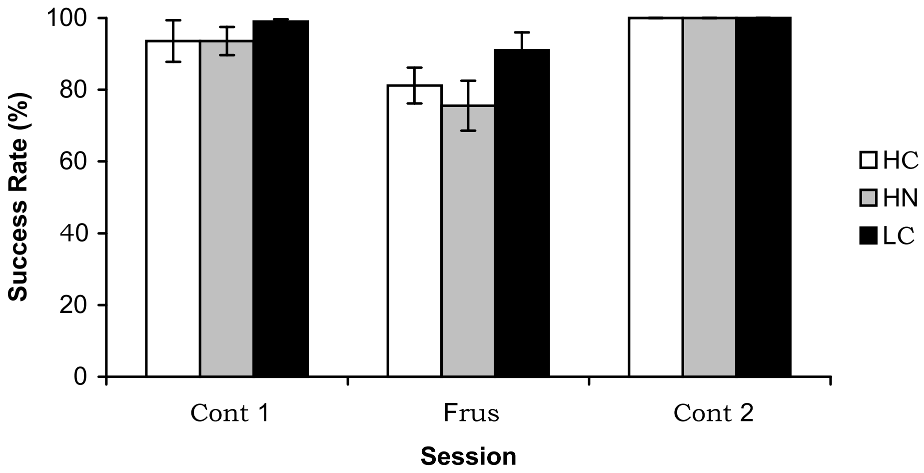

Figure 4.4 Success rate during pre-control (cont 1), frustration (frus) and post-control (cont 2) sessions in experiment 2 in birds from the HFP line from commercial (HC) and semi-natural (HN) rearing conditions and birds from the LFP line from commercial rearing conditions (LC).

In Figure 4.5 the number of key pecks on the most preferred key, the medium preferred key and the least preferred key that was fitted with feathers is shown. Both during control and frustration sessions, the key that was fitted with feathers was avoided.

Discussion

The aim of this experiment was to study the effect of rearing conditions on feather pecking and reaction to frustration and the relationship between them. A comparison was made between birds from the HFP line from commercial (HC) and semi-natural (HN) rearing conditions and birds from the LFP line from commercial (LC) rearing conditions.

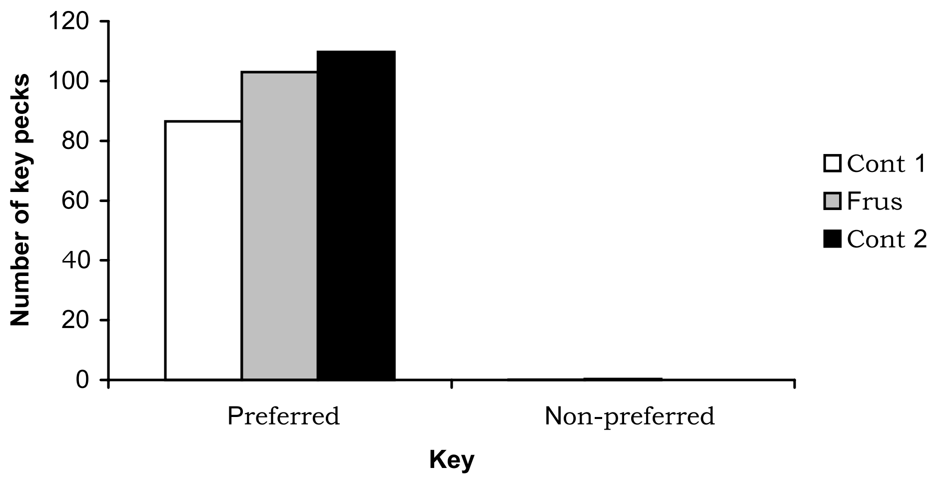

Figure 4.5 Number of key pecks on the preferred keys and the non-preferred key fitted with feathers during pre-control (cont 1), frustration (frus) and post-control (cont 2) sessions.

HN and LC birds were expected to show less feather pecking than HC birds in a feather pecking test. Three HC birds showed severe feather pecking versus one HN bird and zero LC birds. In both HC and HN birds aggressive pecks were observed as well. Almost no aggressive pecking was observed in LC birds. From these results, although limited, it seems that rearing conditions indeed can influence the propensity to develop feather pecking.

During training, LC birds tended to peck more at the keys than HC birds at day 1 and at day 2. LC birds seemed to react sooner on cues in their environment compared with HC birds. Korte et al. (1997) suggested that birds from the HFP line may have a pro-active coping strategy, whereas birds from the LFP line may have a reactive coping strategy. As reactive copers have been found to react more to changes in their environment, the results from our training sessions fit with this suggestion.

In experiment 1, HN birds were expected to show a reaction to frustration similar to LC birds, resulting in high levels of key pecking (Rodenburg et al., 2002), but no differences in key pecking were found. When we distinguished between pecks when the key lights were on and pecks when the key lights were off, an increase as a result of frustration was found for key pecking when the key lights were on. It seems that birds increased their effort to get a food reward at the moment it used to be rewarding, but ceased their efforts in between those moments. The linear decrease over time shows that they tended to give up their efforts towards the end of the frustration session, as may be expected. A decrease was found for the frequency birds put their head in the feeder as an effect of frustration. LC birds tended to put their head more frequently in the feeder then HC birds over all sessions. These results fit with a previous study, in which birds from the LFP line showed more covered feeder pecking, and, hence, put their head in the feeder more frequently then birds from the HFP line during frustration (Rodenburg et al., 2002). The lack of differences in reaction to frustration between birds from different rearing conditions may be caused by the relatively barren environment of the Skinnerbox. In previous research mainly differences as an effect of rearing conditions were found in foraging behaviour and activity in a more complex environment (Wauters et al., 2002). Finally, the fact that HC, HN and LC birds were housed in one group by necessity prior to the experiment may have resulted in less pronounced differences between groups.

In experiment 2, fitting the least attractive key with feathers was expected to attract key pecking behaviour, especially in HC birds. The keys with feathers, however, were avoided both during control and frustration sessions in all cases. In the study by Rodenburg et al. (2002) a bunch of feathers was offered with a similar effect. The bunch was pecked very little and only during frustration. No differences between HFP and LFP lines were found. In another experiment, where an actual bird was present during frustration, and increase in aggressive pecking but also in non-aggressive, gentle and severe feather pecking was observed (Haskell et al., 2000). As Jones (2001) showed that birds prefer static objects to peck at over moving objects, it is unlikely that only the fact that life birds move around causes the differences in reaction. The presence of other birds seems to be very important to trigger pecking behaviour. In an experiment where different tests to measure feather pecking were compared, bunch pecking in an individual test was not a good measure of feather pecking in the homepen. In a social feather pecking test, however, bunch pecking was a good measure of gentle feather pecking in the homepen (Rodenburg and Koene, in press). Results for key pecking in experiment 2 were similar to the results found in experiment 1. Overall birds had lower success rates during the frustration session, compared with both control sessions, as may be expected. HN birds tended to have lower success rates during frustration than HC birds, indicating that they were less persistent in key pecking during frustration.

In conclusion, the results from the feather pecking test, although limited, indicate that HC birds show more severe feather pecking than HN and LC birds. During training we found that LC birds pecked more at the keys on the first days of training, probably because they are more reactive towards cues in their environment. No differences in reaction to frustration were found between birds from different rearing conditions. LC birds put their head in the feeder more frequently than HC birds, as found in a previous experiment. When feathers were applied to the least attractive key, all birds avoided this key. In future experiments, the presence of other birds could be used to study whether feather pecking can be elicited by frustration.

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Chapter 5
Can feather pecking in laying hens be facilitated by short-term frustration?

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Submitted

Abstract

Feather pecking is a major problem in laying hens. Frustration, i.e. omission of expected reward, may play a role in the development of feather pecking. In two experiments, we studied if feather pecking could be facilitated by short-term frustration in birds that had already developed feather pecking prior to the experiment (experiment 1), and in birds that had not developed feather pecking (experiment 2). Furthermore, the motivation to peck a key for a food reward was assessed, as birds that have a stronger motivation may also react stronger to the omission of a reward. We trained birds to peck a key for a food reward in an automated Skinnerbox and tested them in control and frustration sessions. During frustration, the feeder was covered with Perspex. Frustration did not facilitate feather pecking in either experiment. In experiment 1, feather peckers did show more gentle feather pecking and aggressive pecking during some of the control sessions. Furthermore, victims of feather pecking vocalised more than feather peckers. In experiment 2, HFP birds scratched more than LFP birds, indicating differences in motivation for foraging or dustbathing behaviour. LFP birds also had a stronger motivation to peck at a key for a food reward, fitting with previous results where LFP birds showed a stronger reaction to frustration. No evidence was found that feather pecking could be facilitated by short-term frustration in a Skinnerbox. However, differences in reaction to frustration and in motivation to peck a key for a food reward between high and low feather pecking birds indicate that frustration may still play a role in the development of feather pecking.

Introduction

Feather pecking can be characterised as pecking at- and pulling out of feathers of conspecifics and varies from gentle feather pecking to severe feather pecking (Savory, 1995). Severe feather pecking leads to feather damage and feather loss, high feeding costs due to heat loss, and high mortality rates and is considered a major welfare problem. Feather pecking is only seen in birds kept in captivity. There are reports on feather pecking in ostriches (Sambraus, 1995), ducks (Raud and Faure, 1994), Japanese quail (Bilcik and Bessei, 1993), pheasants (Hoffmeyer, 1969) and laying hens (Wennrich, 1975). The causation of feather pecking behaviour varies between species. In laying hens, evidence has been found that feather pecking is redirected ground pecking behaviour, originating either from a foraging (Blokhuis, 1986) or a dustbathing (Vestergaard and Lisborg, 1993) context.

Line differences in feather pecking indicate a genetic background (Hughes and Duncan, 1972). Heritability estimates for feather pecking range from 0.07 to 0.56 (Cuthbertson, 1980; Bessei, 1984; Kjaer and Sørensen, 1997; Rodenburg et al., 2003). Divergent selection on feather pecking has been shown to be feasible (Kjaer et al., 2001). Blokhuis and Beuving (1993) reported differences in feather pecking in two commercial selection lines, selected on production related traits. Therefore these lines were labelled the high (HFP) and low (LFP) feather pecking lines. Line differences in feather pecking have been confirmed both at young age (Riedstra and Groothuis, 2002; Van Hierden et al., 2002a) and at adult age (Rodenburg and Koene, 2003). Furthermore, line differences in corticosterone response to manual restraint have been shown (Korte et al., 1997; Van Hierden et al., 2002b). In a previous study, we found that HFP birds showed a large increase in vocalisations over repeated testing in an individual test, whereas LFP birds showed a decrease (Rodenburg and Koene, 2003).

Frustration, i.e. omission of expected reward, may influence redirection of pecking behaviour. Lindberg and Nicol (1994) proposed a model, in which frustration, for instance because a bird tries to reach the feeder but is unsuccessful, leads to increased arousal, fear and aggression. Under these circumstances, occasional pecks at the plumage may develop into damaging feather pecking.

Line difference in feather pecking may be caused by an underlying difference in reaction to frustration (Lindberg and Nicol, 1994). From previous studies, we concluded that pecking at feathers in an individual context is not comparable with feather pecking in a social context (Rodenburg et al., 2002; Rodenburg and Koene, 2003). Frustration may still play a role in the development of feather pecking, but this should be studied using test birds accompanied by other birds, the so-called companion birds.

Reaction to frustration may also be influenced by the motivation a bird has to obtain a certain commodity. If a bird has a stronger motivation to peck a key for a food reward than another bird, it may also show a stronger reaction to frustration, i.e. the omission of that food reward.

The aim of the present experiment was to study if feather pecking can be facilitated by frustration in birds that had already developed feather pecking prior to the experiment (experiment 1), and in birds that had not developed feather pecking (experiment 2). In both experiments, reaction to frustration was studied with and without another bird present. When no other bird was present, key pecking, covered feeder pecking and redirected pecking were studied. Also vocalisations were recorded, as they can be used as welfare indicators in laying hens (Zimmerman and Koene, 1998). When another bird was present, it was expected that pecking would be redirected at the bird in birds with a strong propensity to display feather pecking. In experiment 2, repeated frustration was used, to study if this can facilitate the development of feather pecking in birds from the HFP line, that had not developed feather pecking prior to the experiment. Furthermore, the maximum number of times that HFP and LFP birds would peck for a food reward was assessed. LFP birds were expected to have a stronger motivation to peck a key for a food reward, as LFP birds showed a stronger reaction to frustration in a previous study (Rodenburg et al., 2002).

Methods Experiment 1

Animals and housing

For experiment 1, 20 White Leghorn laying hens were selected either as feather peckers or victims of feather pecking. They originated from an F2-cross of high and low feather pecking lines. Selection was based on levels of giving and receiving severe and gentle feather pecks in a social feather pecking test at 30 weeks of age. In this feather pecking test, pecking behaviour of a group of five birds was observed for 30 minutes (Rodenburg et al., 2003). Birds that were both feather peckers and victims were excluded from either group. Six additional birds from the same population were used as companion birds. These birds were selected on performing little to no severe feather pecking, to avoid severe feather pecking from the companion bird on the test bird.

Feather pecking behaviour of feather peckers, victims and companion birds is shown in Table 5.1.

Table 5.1 Mean number of bouts of gentle and severe feather pecking per 30 minutes as a feather pecker (F gentle and F severe) and as a victim (V gentle and V severe) in the birds selected for experiment 1.

Group	N	F gentle	F severe	V gentle	V severe
Feather peckers	10	2.3	4.3	0	0
Victims	10	0.1	0	2.8	2.8
Companion	6	1.9	0.6	2.4	3.3

Birds were housed in cages of the type described by Van Liere and Wiepkema (1992), measuring 100 x 50 x 50 cm (l x w x h). Each cage was equipped with a dustbath and a nestbox and had a partly slatted floor. Food and water were available ad libitum. Lights were on from 3:00 until 19:00. The Wageningen University Committee on Animal Care and Use has approved experiment 1 and 2.

Apparatus

Three automated Skinnerboxes were used of the type described by Zimmerman and Koene (1998). They were located in a sound attenuated room, close to the homecages. Each Skinnerbox measured 60 x 50 x 65 cm. Three lighted keys were present 10 cm apart on the intelligence panel, 26 cm above the floor. The feeder was accessible through a round hole (12 cm in diameter) in the centre of the intelligence panel, 10 cm above the floor. Food was only accessible when the feeder was raised. The presence or absence of a bird's head in the feeder was detected by a photocell. A 5-W house-light was fixed 8 cm above each Skinnerbox. The Skinnerboxes were operated through a custom-made program, using LabView® software (National Instruments, 1994). Changes in key lights (on or off), keys (peck or no peck) and photocells (head or no head) were automatically recorded and stored on disk. Skinnerboxes and computer were located in the same room.

Training procedure

Each bird was habituated to a Skinnerbox for 15 minutes on the first day of shaping. On the following days, each bird was food deprived (23 hours per day throughout the experiment) and auto-shaping was used to train the birds to press one of the three keys for a food reward. During auto-shaping all keys were illuminated every 30 ± 2 s. The keys were illuminated for 10 s and after that, the feeder was raised and the bird was allowed to eat for 5 s (classical conditioning). This auto-shaping procedure can be used to train birds to peck a key through pairings of illumination of that key with food (Lieberman, 1993, pp. 96-97). When all birds were pecking at the keys during auto-shaping, each bird was trained to peck a key when the stimulus lights were on, using operant training. They were trained for 15 min per day. The house-light was on from the start to the end of each session. The training sessions were identical to the auto-shaping sessions, only during training birds had to press one of the keys to obtain a food reward. Each bird was trained until the training criterion was reached: at least 95% correct key pecks and head in feeder within 2 sec after the feeder was raised. Two birds from the group of victims did not reach the training criterion. Hence, 10 feather peckers and 8 victims were subjected to the test procedure.

Test procedure

Birds were tested between 10:00 and 16:00 to avoid interference with egg laying. After each session, food was available for 45 minutes. After that, birds were food deprived for another 23 hours. Birds were subjected to three 15-min test sessions of approximately 30 trials each: a pre-control session, a frustration session and a post-control session. Food was normally accessible during both control sessions. During the frustration session the feeder was covered with Perspex®, allowing the birds to see the food, but not to reach it. These three sessions were repeated in the two subsequent weeks in the presence of a companion bird. On the first day of each of these two weeks, birds were habituated to one specific companion bird. On day 2, 3 and 4 the control and frustration sessions as described before were repeated in the presence of this companion bird. In the second week, the same procedure was followed, but with a different companion bird. Behaviour was recorded on videotape and analysed with The Observer® programme (Noldus, 1993) using focal sampling. The ethogram is described in Table 5.2.

Table 5.2 Ethogram experiment 1 and 2

Behaviour	Description
Key peck	Peck at one of the keys
Covered feeder peck[a]	Peck at the covered feeder
Redirected peck	Peck at other parts of Skinnerbox
Scratch	Backward stroke with one leg
Escape Movement	Pacing in front of the exit
Pacing	Pacing in front of the keys
Alarm call	[Kot kot kot kodeek]
Gakel call	[Pwook pwok pwok pwok]
Aggressive peck	Peck at head or neck of companion bird
Gentle feather peck	Small neck movement, no reaction victim
Severe feather peck	Large neck movement, reaction victim

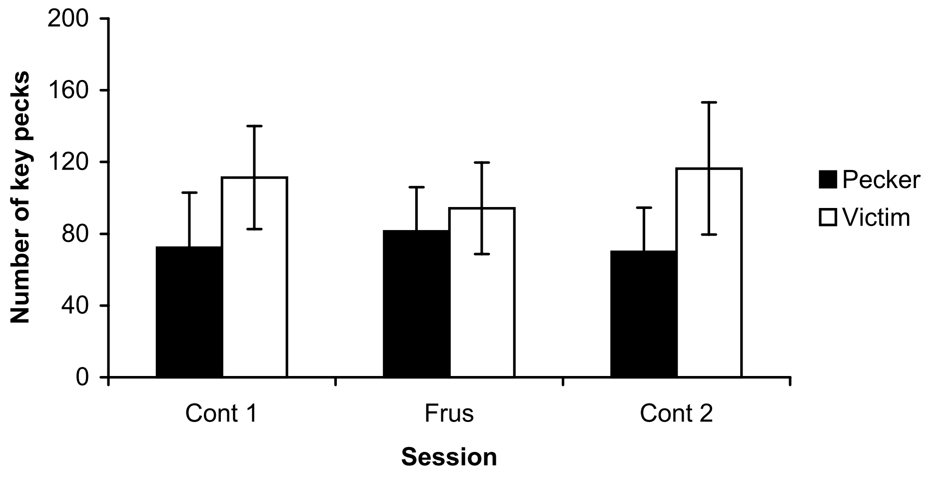
[a] Only possible during the frustration session

Statistical analysis

Analysis of variance was performed using the GLM-procedure in the SAS® statistical programme (SAS, 1996). Frequencies and durations of all observed behaviours were transformed with a square root transformation or an arcsine square root transformation respectively, to realise normal distributions. Group (feather pecker or victim) was the only fixed effect included in the model. Since feather peckers and victims of feather pecking were tested alternately, testing order was not included. To compare the frustration session to both control sessions, sessions were analysed as repeated measures.

Results

No differences were found in number of key pecks between feather peckers and victims of feather pecking, nor between control and frustration sessions (Figure 5.1). Birds showed more redirected pecking during the frustration sessions compared with both control sessions ($F_{1,16} = 15.62$; $P<0.01$).



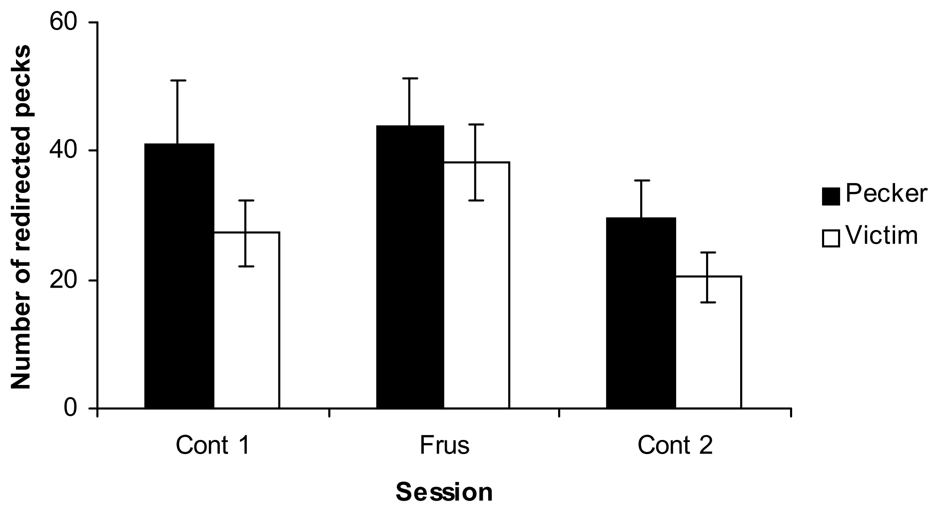


Figure 5.1 Mean number of key pecks (top panel) and redirected pecks (bottom panel) in feather peckers and victims of feather pecking in the control (cont 1 and 2) and frustration (frus) sessions without a companion bird.

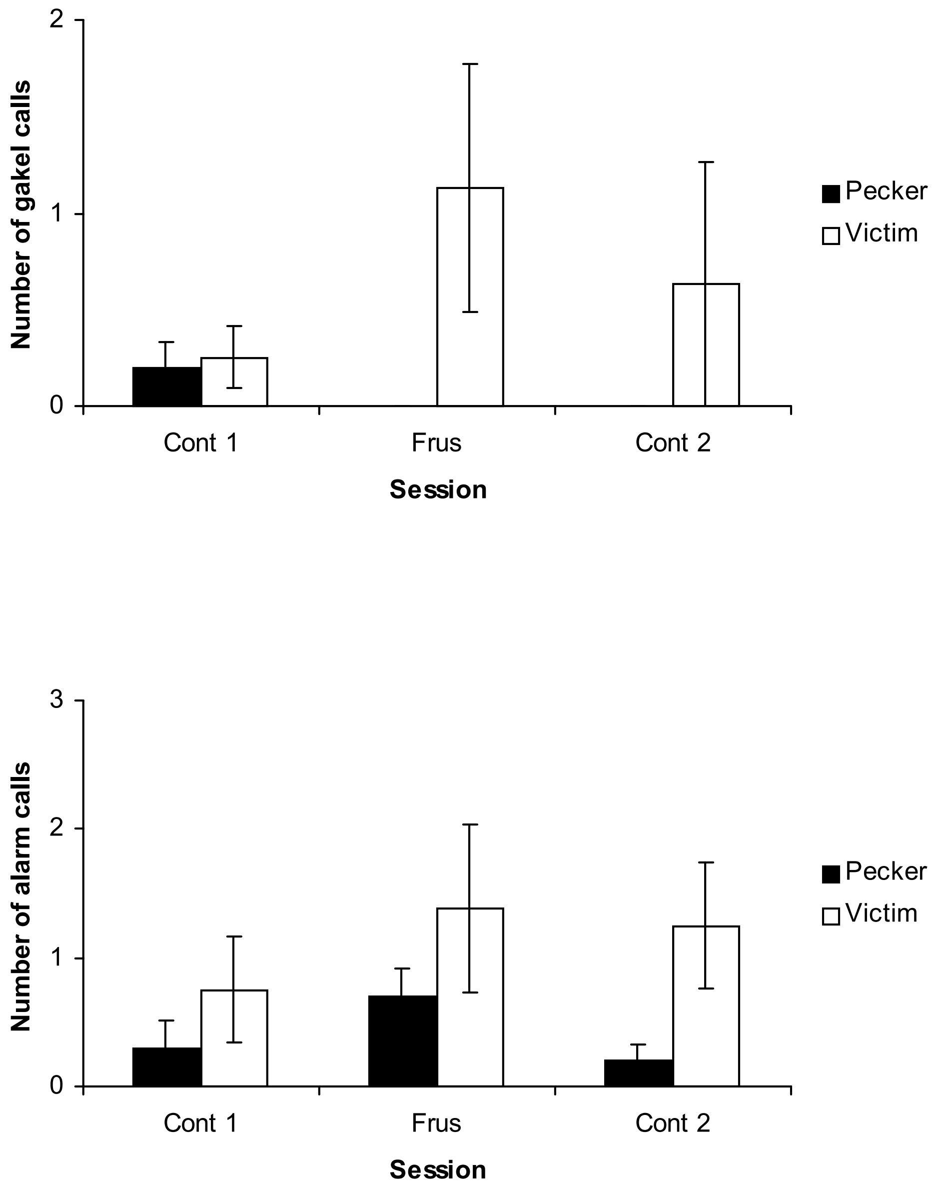


Figure 5.2 Mean number of gakel calls (top panel) and alarm calls (bottom panel) in feather peckers and victims of feather pecking in the control (cont 1 and 2) and frustration (frus) sessions without a companion bird

No difference was found in covered feeder pecking during the frustration session between feather peckers (mean 15.6 ± 2.4) and victims (mean 17.9 ± 3.4).

The mean number of gakel calls and alarm calls in feather peckers and victims of feather pecking in the control and frustration sessions without a companion bird are shown in Figure 5.2. The total number of vocalisations recorded was low in all three sessions. During the frustration session, victims of feather pecking produced more gakel calls than feather peckers ($F_{1,16}$= 4.73; P<0.05). Victims also produced more alarm calls than feather peckers during the second control session ($F_{1,16}$= 5.26; P<0.05).

Levels of gentle feather pecking were low in week 1 and no increase was found as an effect of frustration (Figure 5.3). In week 2, there was a tendency for a linear increase in gentle feather pecking ($F_{1,16}$ = 3.66; P<0.10). In the first control session in week 2, feather peckers showed more gentle feather pecking than victims ($F_{1,16}$ = 4.88; P<0.05). For severe feather pecking, there was a large increase for the feather peckers in the frustration session in week 1, but the difference was not significant, as it was only one bird performing 141 severe pecks in this session. The same bird showed a high level of severe feather pecking (130 pecks) during the habituation session in week 2. Levels of severe feather pecking were higher in week 2 than in week 1. Feather peckers tended to show more aggressive pecking than victims during the second control session in week 1 ($F_{1,16}$ = 3.32; P<0.10). Furthermore, victims showed an increase in aggression as a result of frustration, whereas the level of aggression in feather peckers stayed the same compared with the control session ($F_{1,16}$ = 7.01; P<0.05).

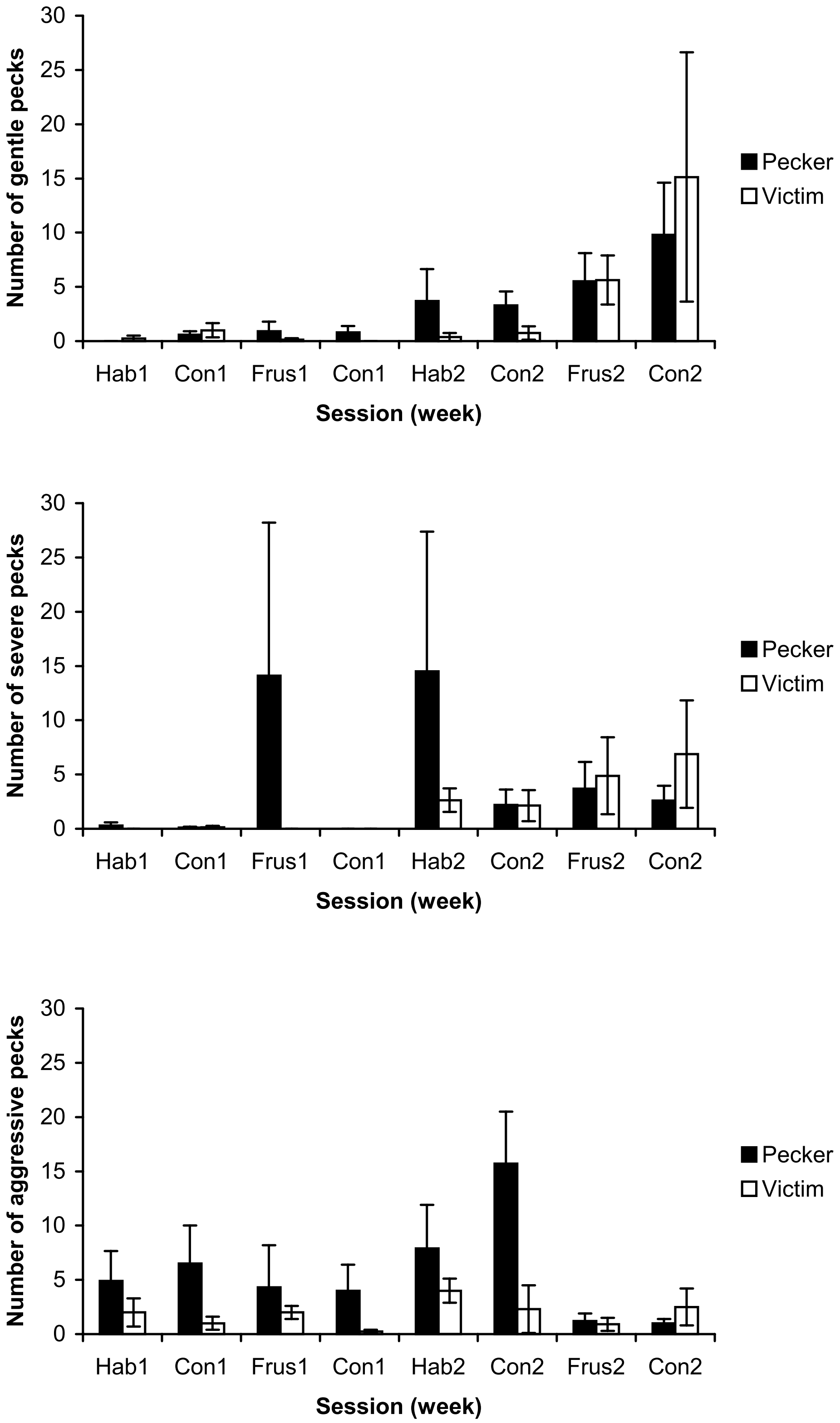


Figure 5.3 Mean number of gentle feather pecks (top panel), severe feather pecks (middle panel) and aggressive pecks (bottom panel) in feather peckers and victims of feather pecking in habituation (hab), control (con) and frustration (frus) sessions in week 1 and week 2 with a companion bird.

Methods Experiment 2

Animals and housing

Thirty beak-trimmed White Leghorn laying hens of 18 weeks old were obtained from Hendrix Poultry Breeders, Boxmeer, The Netherlands. These hens originated from two commercial selection lines, the so-called high and low feather pecking lines. These lines were selected for production related traits, but they also showed a difference in feather pecking behaviour (Riedstra and Groothuis, 2002; Van Hierden et al., 2002a; Rodenburg and Koene, 2003). These lines were also used to make the cross population, from which birds were used in experiment 1. In experiment 1 birds were selected on phenotype (feather peckers or victims), in experiment 2 on genotype (high or low feather pecking line).
After arrival at the research accommodation, each bird was marked individually with a wing tag and housed individually in the same cages as described in experiment 1. Birds were fed restrictedly at 75% of their food intake when fed ad libitum. This was done by measuring each bird's food intake at 19 weeks of age. From 25 weeks of age, food ratios were adjusted according to a standard scheme from Hendrix Poultry Breeders, Boxmeer, The Netherlands, correcting for each bird's body weight. Lights were on from 3:00 until 18:00.

Habituation and training

For experiment 2, the same three automated Skinnerboxes were used as in experiment 1.
Each bird was habituated to a Skinnerbox for 15 minutes on the first- and on the second day of shaping. After two days of habituation, birds were fed restrictedly and trained to peck a key in the Skinnerbox using autoshaping (see experiment 1 for autoshaping procedure). After each bird had been subjected to 14 autoshaping sessions, six sessions of operant training followed (see experiment 1). During these sessions, a bird had to peck a key when the stimulus lights were on. After these sessions, birds that were unable to perform the task were trained using hand shaping, followed again by operant training for all birds. After operant training and hand shaping, birds were habituated to the

presence of a companion bird during two consecutive days. These habituation sessions were also used to select the companion birds that would be used in the test sessions. A companion bird was selected when it did not show any aggressive behaviour. At the last two days of training and habituation, each bird was required to reach the training criterion: at least 95% correct key pecks and head in feeder within 2 s after the feeder came up on both days.

Test procedure

During the test sessions, birds were still fed restrictedly at 75% and subjected to five 15-min test sessions of approximately 30 trials each: a control session on Monday and four frustration sessions on the four subsequent weekdays. A factorial arrangement was used with line (HFP or LFP) and companion bird (present or not present) as factors. Five birds per line were tested with a companion in week 1 and without a companion bird in week 2 and five birds per line were subjected to the reverse order of testing. The order in which the birds were tested was kept the same during the experiment. Food was normally accessible during the control session. During the frustration sessions the feeder was covered with Perspex®, allowing the birds to see the food, but not to reach it. Birds were tested between 10:00 and 16:00 to avoid interference with egg laying. After each session, birds received their daily food ration. Behaviour was recorded on videotape and analysed with The Observer® programme (Noldus, 1993) using focal sampling. The ethogram was the same as used in experiment 1 (Table 5.2).

Pecking for food

Three days after the repeated frustration experiment, the maximum number of key pecks a bird would give to obtain a food reward was measured in the same 21 birds. Birds were still fed 75% of ad libitum. They were re-trained to peck at the left key only, because the computer programme used could operate only the left key. After this training day, birds were subjected in random order to a +2 progressive ratio or a +4 progressive ratio, e.g. the number of pecks required to obtain a food reward incremented with two or with four pecks after each rewarded trial. Maximum session time was 30 minutes, but a session was also ended when a bird failed to obtain a reward and also failed in the subsequent trial. After the two test days, birds were fed unrestrictedly for four days. Then, birds were tested again under unrestricted feed conditions using a +2 progressive ratio.

Statistical analysis

Analysis of variance was performed using the GLM-procedure in the SAS® statistical programme (SAS, 1996). Frequencies and durations of all observed behaviours were transformed with a square root transformation or an arcsine square root transformation respectively, because data were not distributed normally. Line, testing order (first with companion and than without companion and vice versa), and time of testing were included in the model as fixed effects. The effect of frustration was calculated by comparing the first frustration session to the control session. The effect of repeated frustration was calculated by analysing the four subsequent frustration sessions as repeated measures. For the pilot experiment to measure each bird's motivation to work for food, the maximum number of pecks that each bird delivered in each of the three test sessions was calculated. Data were analysed with line and time of testing as fixed effects.

Results

Key pecking showed a linear decrease over the repeated frustration sessions ($F_{1,11} = 24.25$; $P<0.001$; Figure 5.4). Redirected pecking showed a linear increase from the first through the fourth frustration session ($F_{1,11} = 11.03$; $P<0.01$). Levels of covered feeder pecking were highest during the first frustration session. Over the repeated frustration sessions, a linear decrease was found for covered feeder pecking ($F_{1,11} = 25.38$; $P<0.001$). LFP birds pecked more on the covered feeder than HFP birds, but the difference was not significant ($F_{1,12} = 1.24$; $P=0.29$). No line differences were found in reaction to frustration in the sessions without a companion bird.

HFP birds scratched more than LFP birds over all sessions ($F_{1,12}=11.67$; $P<0.01$; Figure 5.5). A decrease of scratching behaviour was found from the control session to the first frustration session

($F_{1,12}$=20.18; P<0.001) and over the repeated frustration sessions an overall line difference was found ($F_{1,12}$=11.67; P<0.01). No line differences were found for time spent pacing or time spent making escape movements. Time spent pacing in front of the keys showed a linear decrease over repeated frustration ($F_{1,12}$=5.66; P<0.05), whereas time spent making escape movements in front of the entrance of the Skinnerbox increased as an effect of frustration. This increase, however, was not significant.

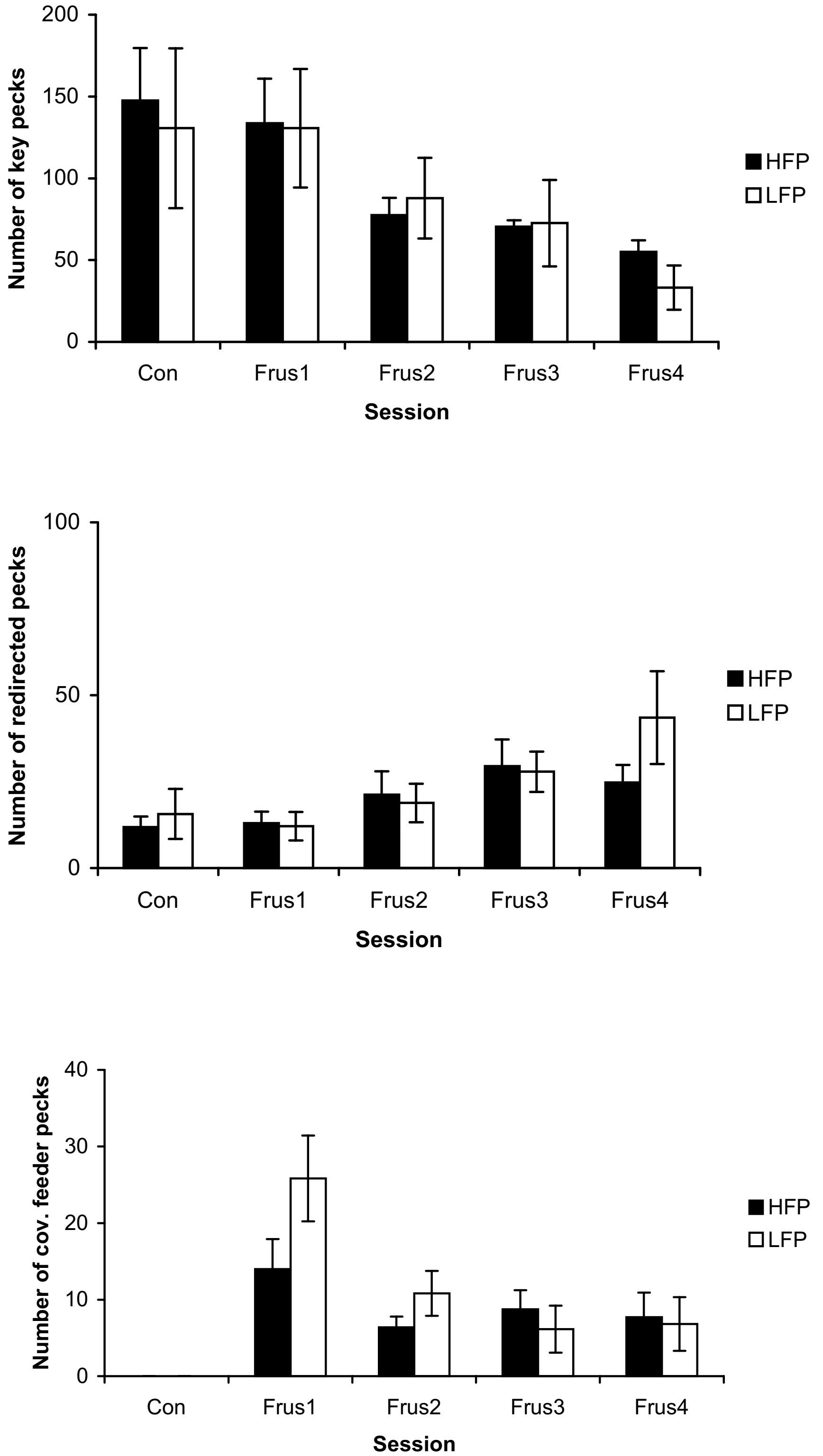


Figure 5.4 Mean number of key pecks (top panel), redirected pecks and covered feeder pecks (bottom panel) in HFP and LFP birds during control (con) and repeated frustration sessions (frus 1-4) without a companion bird.

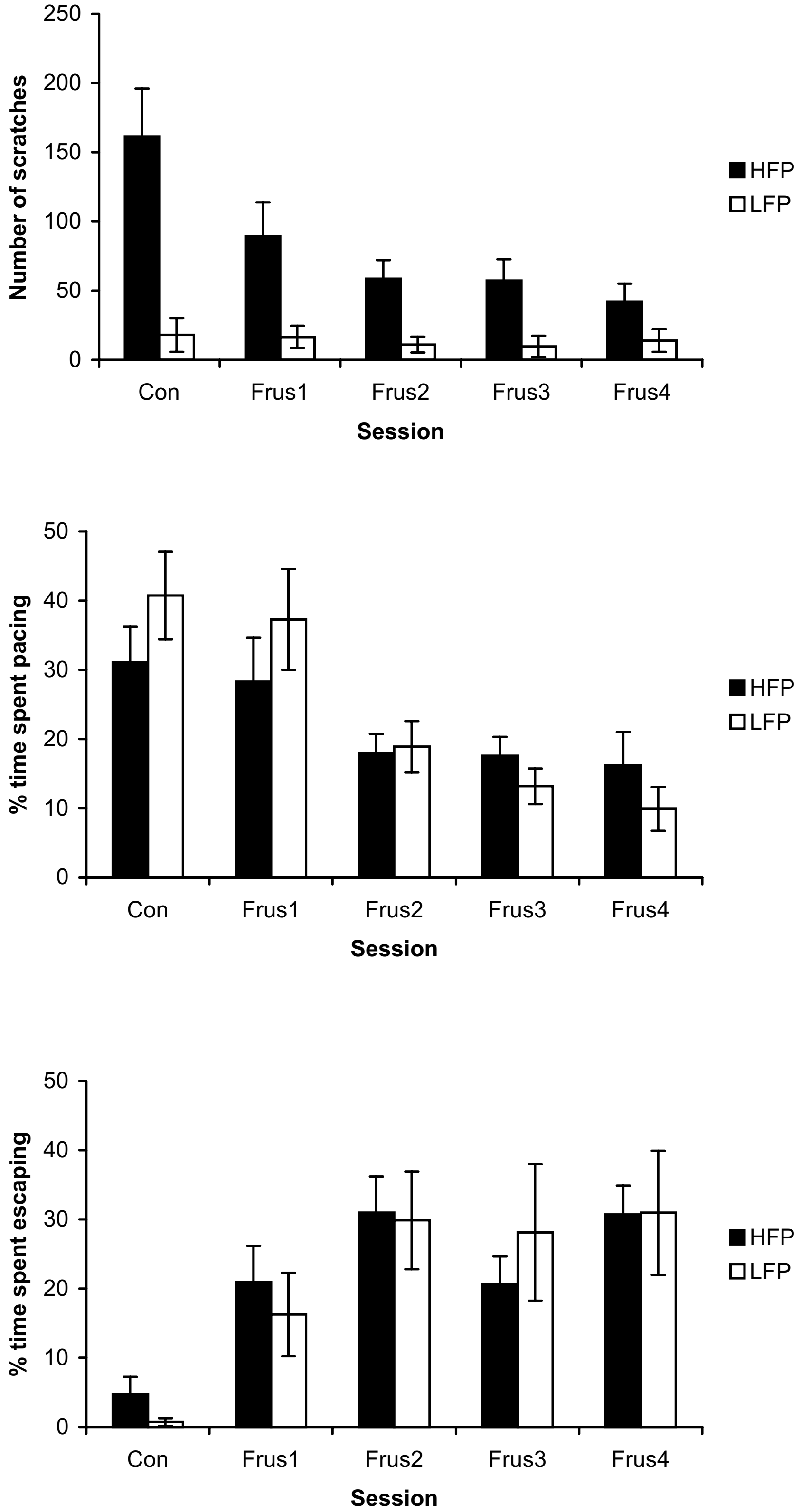


Figure 5.5 Mean number of scratches (top panel) and the time spent pacing (middle panel) and the time spent making escape movements (bottom panel) in HFP and LFP birds during control (con) and repeated frustration sessions (frus 1-4) without a companion bird.

The mean number of gentle feather pecks and aggressive pecks in HFP and LFP birds during control and repeated frustration sessions with a companion bird are shown in Figure 5.6. Levels of feather pecking were low in this experiment. In fact, severe feather pecking was not observed at all. Gentle feather pecking was only observed during the frustration sessions, but levels were low and no differences were found between HFP and LFP birds. Aggressive pecking was observed both during control and frustration sessions. There was a slight but non-significant increase in the first frustration session and a slight decrease over repeated frustration ($F_{1,12}$= 2.31; P=0.15).

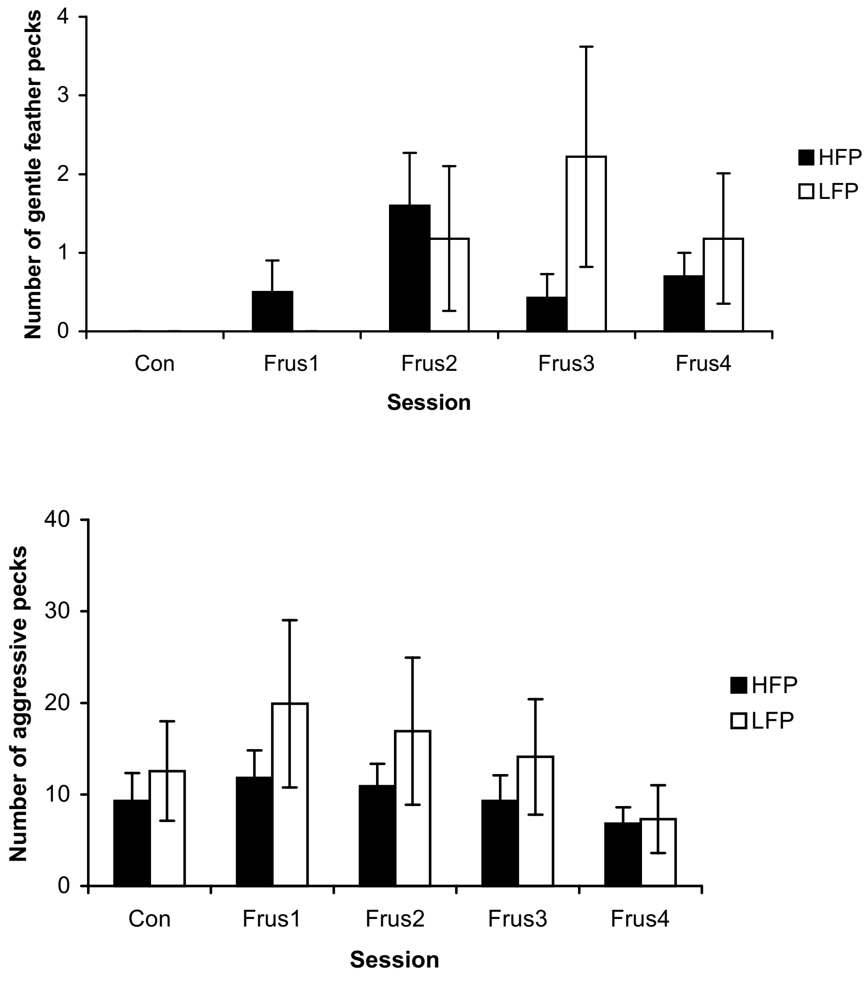


Figure 5.6 Mean number of gentle feather pecks (top panel) and aggressive pecks (bottom panel) in HFP and LFP birds during control (con) and repeated frustration sessions (frus 1-4) with a companion bird.

The maximum number of key pecks given to obtain a food reward in HFP and LFP lines under +2 restricted, +4 restricted and +2 unrestricted progressive ratios is shown in Figure 5.7. LFP tended to give a higher maximum number of key pecks for a food reward than HFP birds under +2 restricted ($F_{1,19}$= 3.78; P<0.10), and under +2 unrestricted ($F_{1,19}$= 3.93; P<0.10) conditions.

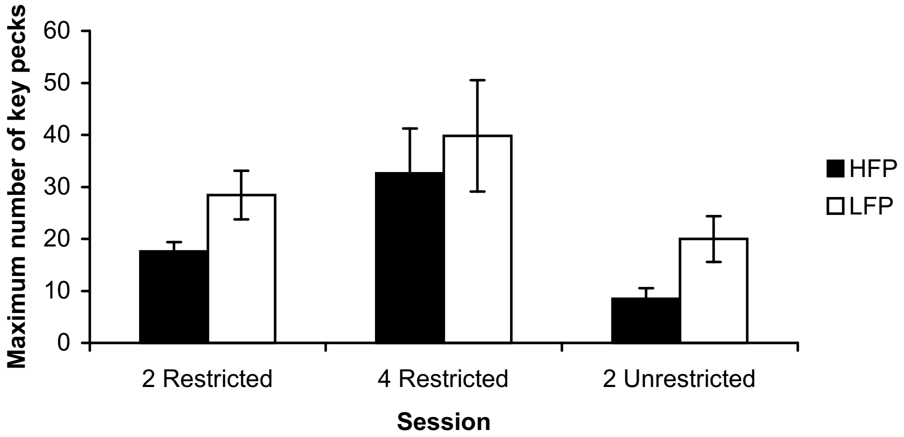


Figure 5.7 Maximum number of key pecks given for a food reward in HFP and LFP lines under +2 restricted, +4 restricted and +2 unrestricted progressive ratios.

Discussion

The aim of the present experiment was to study whether feather pecking can be facilitated by frustration in birds that had already developed feather pecking prior to the experiment (experiment 1), and in birds that had not (experiment 2). In each experiment reaction to frustration was studied without and with a companion bird present. In experiment 1, feather peckers were expected to show a stronger reaction to frustration and to show feather pecking during frustration in the presence of a companion bird. In experiment 2, repeated frustration was expected to facilitate the development of feather pecking in HFP birds. Finally, LFP birds were expected to have a stronger motivation to peck a key for a food reward than HFP birds, as they also showed a stronger reaction to frustration in a previous study.

In experiment 1, there was a large increase of severe feather pecking for feather peckers in the frustration session in week 1, but the difference was not significant as it was only one bird performing severe feather pecking in this session. Levels of gentle feather pecking were not affected by frustration. In experiment 2, levels of feather pecking were low. In fact, severe feather pecking was not observed at all. Gentle feather pecking was only observed during the frustration sessions, but levels were low and no differences were found between HFP and LFP birds. These results showed that short-term frustration could not facilitate feather pecking in feather peckers and victims of feather pecking or in HFP and LFP birds that had not developed feather pecking prior to the experiment using repeated frustration. In the study by Lindberg and Nicol (1994), feather pecking did develop over time and groups with operant feeders showed more feather pecking than groups with normal feeders. In another study, where a dominant test-bird was frustrated in a runway in the presence of a sub-dominant companion bird, both aggression and feather pecking were observed as an effect of frustration (Haskell et al., 2000). The fact that we did not find similar results might be caused by the fact that we still used relatively short frustration sessions, although we used repeated sessions in experiment 2. Furthermore, the observations by Lindberg and Nicol (1994) took place in the homepen. Development of feather pecking in a group of birds in their home environment may be very difficult to imitate in the artificial Skinnerbox environment. The problem may be similar to the problem we encountered when comparing different tests to measure feather pecking, where bunch pecking in an individual test was not comparable with feather pecking in the homepen (Rodenburg and Koene, 2003).

In experiment 1, feather peckers did show more gentle feather pecking and more aggressive pecking than victims during some control sessions, but no significant difference in severe feather pecking was found. In the present study, levels of aggression were low in victims, but not in feather peckers, as can be seen in Figure 5.3. Victims showed an increase in aggression in reaction to frustration in week 1, whereas feather peckers showed a higher level of aggression throughout the whole experiment. In experiment 2, aggressive pecking was observed both during control and frustration sessions. There was a slight but non-significant increase in the first frustration session and a decrease over repeated frustration. Aggressive pecking and feather pecking are distinct forms of pecking (Savory, 1995). It may be, however, that feather peckers are also the most aggressive birds. Frustration induced aggression has been described in pigs (Arnone and Dantzer, 1980), as well as in laying hens (Duncan and Wood-Gush, 1971; Haskell et al., 2000). In experiment 1, it seems that only victims showed frustration induced aggression, whereas feather peckers showed aggression irrespective of the session. In experiment 2, the difference between control and frustration was not significant.

In the sessions without a companion bird in experiment 1, no differences were found in number of key pecks between feather peckers and victims of feather pecking, nor between control and frustration sessions. Birds showed more redirected pecking during the frustration sessions compared with both control sessions. No difference was found in covered feeder pecking during the frustration session between feather peckers and victims. In experiment 2, key pecking and covered feeder pecking showed a linear decrease over the repeated frustration sessions, whereas redirected pecking showed a linear increase. No line differences were found in reaction to frustration in the sessions without a companion bird. Although LFP birds showed more covered feeder pecking than HFP birds during the first frustration session, as was found in a previous study (Rodenburg et al., 2002), this difference was not significant. In both experiments, redirected pecking increased as an effect of frustration, as was also found by Duncan and Wood-Gush (1972).

In experiment 1, differences were found in vocalisations. During the frustration session, victims of feather pecking produced more gakel calls than feather peckers. Victims also produced more alarm calls than feather peckers during the second control session. Zimmerman and Koene (1998) showed the number of gakel calls increased as an effect of frustration, whereas alarm-calls were recorded both during control and frustration sessions and seem to indicate anxiety. The results from the present study indicate that victims of feather pecking are more affected by omission of expected reward than feather peckers and that they show higher levels of anxiety, as indicated by the number of alarm calls in the second control session. Rodenburg and Koene (2003) showed that birds from the HFP line showed an increase in vocalisations over repeated testing in an individual test, whereas birds from the LFP line showed a decrease. This line difference, however, may not be directly related with feather pecking.

Furthermore, it is difficult to compare these tests, as in the present study birds were tested in the presence of a companion, as compared with isolation.

In experiment 2, HFP birds scratched more than LFP birds over all sessions. A decrease of scratching behaviour was found from the control session to the first frustration session and over the repeated frustration sessions an overall line difference was found. Adversely to the line difference we found, Klein et al. (2000) showed that a strain that showed higher levels of feather pecking than other strains spent less time scratching. Feather pecking has been shown to be redirected ground pecking, deriving either from a foraging (Blokhuis, 1986) or a dustbathing (Vestergaard and Lisborg, 1993) context. As scratching is part of both foraging and dustbathing behaviour, it could be that HFP birds are more motivated for these behaviours and hence more likely to develop feather pecking. Results from other studies, however, showed that LFP birds performed more foraging behaviour than HFP birds (Van Hierden et al., 2002a; Rodenburg and Koene, 2003). These results are from homepen observations, however, and are not comparable with pecking behaviour in a Skinnerbox.

Pacing and making escape movements were the only behaviours in experiment 2 where a clear effect of repeated frustration was found. Time spent pacing in front of the keys showed a linear decrease over repeated frustration, whereas time spent making escape movements in front of the entrance of the Skinnerbox increased as an effect of frustration. It seems that over the repeated frustration sessions, birds tended to loose their interest in the control panel of the Skinnerbox, as this was no longer rewarding, and were more interested in escaping the Skinnerbox environment to return to the homepen, as may be expected.

Finally, when the motivation to work for food in HFP and LFP birds was assessed, we found that LFP tended to give a higher maximum number of pecks for a food reward than HFP birds, both under +2 restricted, and under +2 unrestricted progressive ratios, as hypothesised. These results fit well with our previous findings, as LFP birds also have been found to react stronger to frustration, indicated by higher levels of covered feeder pecking and key pecking (Rodenburg et al., 2002).

In conclusion, no evidence was found that feather pecking could be facilitated by short-term frustration in a Skinnerbox, neither in feather peckers and victims of feather pecking, nor in naive HFP and LFP birds using repeated frustration. However, differences in reaction to frustration between feather peckers and non-feather peckers in both experiments indicate that frustration may still play a role in the development of feather pecking. Victims of feather pecking vocalised more than feather peckers, both during control and frustration sessions, whereas feather peckers showed more gentle feather pecking and aggressive pecking during some of the control sessions. In experiment 2, HFP birds scratched more than LFP birds, indicating differences in motivation for foraging or dustbathing behaviour. Furthermore, LFP birds tended to deliver a higher maximum number of pecks for a food reward, fitting with previous results where LFP birds showed a stronger reaction to frustration. In future research, models using long-term frustration in the homepen should be used to study the relationship between feather pecking and frustration further.

Acknowledgements

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Chapter 6
Heritability of feather pecking and open-field response in laying hens at two different ages

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Abstract

The objective of the current study was to estimate heritabilities (h^2) of feather pecking and open-field response in laying hens at two different ages. An F_2 cross, originating from a high and a low feather pecking line of laying hens, was used for the experiment. Each of the 630 birds of the F_2 cross was subjected to an open-field test (individual, 10 min) at 5 and 29 weeks of age, and to a social feather pecking test (groups of 5 birds on wood shavings, 30 min) at 6 and 30 weeks of age. Both tests were performed in a square open-field (1.25 x 1.25 m). Behaviour was recorded directly from a monitor. Heritabilities of feather pecking and open-field behaviours were calculated. In the open-field test at 5 weeks of age, high h^2 were found for most traits, ranging from 0.20 for the frequency of flying to 0.49 for number of steps. In the social test at 6 weeks, gentle feather pecking (0.12) and ground pecking (0.13) were found to be heritable. When both tests were repeated at 29 and 30 weeks of age, h^2 estimates were lower for the open-field test, ranging from 0.10 for duration of sitting to 0.20 for latency to first step. In the social test, however, higher h^2 estimates of 0.15 for gentle feather pecking and 0.30 for ground pecking were found compared with 6 weeks of age. In conclusion, gentle feather pecking and open-field behaviours may be used in selection against feather pecking.

Introduction

Feather pecking impairs animal welfare and results in higher feeding costs and increased mortality rates in laying hens. It is characterised by pecking at- and pulling of feathers of other birds. Feather removal has been shown to be painful (Gentle and Hunter, 1990) and results in bald patches. This feather damage as a result of feather pecking can lead to a heat loss resulting in 20% higher energy requirements (Blokhuis and Wiepkema, 1998). The bald patches may attract tissue pecking, resulting in wounded birds that may be pecked to death (Savory, 1995). Feather pecking is a problem in all currently used housing systems for laying hens, but in large group housing systems the problem is more difficult to control. The current development in the European Union from beak-trimmed birds in battery cages towards large group housing with birds with intact beaks asks for tools to control feather pecking. In the United States, guidelines developed by large fast-food chains in co-operation with scientists (Rahn, 2001) may steer future egg production systems in the same direction as in the European Union.

Line differences in both plumage condition (Ambrosen and Petersen, 1997; Wahlstrom et al., 2001) and in feather pecking behaviour (Hughes and Duncan, 1972) suggest a genetic background. Direct selection has been shown to be feasible, using either individual selection against feather pecking (Kjaer et al., 2001) or group selection against mortality (Craig and Muir, 1993; Muir, 1996). Craig and Muir (1993) reported a high realised family heritability (h^2) of 0.65 for days without beak-inflicted injuries. Three studies have reported h^2 of feather pecking based on direct observation of pecking behaviour (Cuthbertson, 1980; Bessei, 1984; Kjaer and Sørensen, 1997). In these studies, h^2 for performing feather pecking ranged from 0.07 to 0.56 and for receiving feather pecking from 0.00 to 0.15. None of these studies distinguished between the different forms of feather pecking, i.e. gentle and severe feather pecking (Savory, 1995). This distinction may be important, as gentle and severe feather pecking may have different ways of developing and may be differently affected by genetic and environmental factors. Recently, it has been suggested that gentle feather pecking at young age may develop into stereotyped gentle feather pecking or into severe feather pecking in adult laying hens by either increased intensity or increased severity of bird-to-bird pecks (McAdie and Keeling, 2002).

Feather pecking has also been associated with fearfulness (Hughes and Duncan, 1972) and, more recently, with open-field response (Jones et al., 1995) and coping strategy (Korte et al., 1997). The open-field test has been used for the study of emotional reactivity and motivation in laboratory animals, but also in poultry (Candland and Nagy, 1969). Gallup and Suarez (1980) proposed that open-field behaviour in poultry is a compromise between opposing tendencies in a bird to return to its flock-mates and to minimise detection by predators (experimenter). Some studies have estimated h^2 for open-field behaviours, with estimates for overall locomotion ranging from 0.08 to 0.49 and for defecation from 0.06 to 0.10 (Boyer et al., 1970; Faure, 1981; Webster and Hurnik, 1989). Jones et al. (1995) showed that birds from a low feather pecking line vocalised and walked sooner in an open-field than birds from a high feather pecking line, reflecting differences in social motivation to return to their flock-mates. Thus the open-field response may be useful as a predictor of feather pecking behaviour and the open-field test may be used to select against feather pecking.

The aim of the present experiment was to estimate h^2 of open-field response at 5 and 29 weeks of age and of feather pecking at 6 and 30 weeks of age. A distinction was made between gentle and severe feather pecking, as they may be differently affected by genetic and environmental factors. The current study may give a better understanding of the possibilities to select against feather pecking either by direct observation of feather pecking or selection on related characteristics using the open-field test. This may eventually enable the breeding of birds that are better adapted to future housing systems.

Materials and methods

Genetic Stock and Population Structure

Two selection lines from a commercial breeder were used for this experiment. These lines have been selected for production related traits, but also differ consistently in feather pecking behaviour: the high and low feather pecking lines (Rodenburg and Koene, 2001; Riedstra and Groothuis, 2002; Van Hierden et al., 2002). A reciprocal cross of these lines was made: six high feather pecking males and six low feather pecking females were used to produce the high x low cross and six low feather pecking males and six high feather pecking females were used to produce the low x high cross. This resulted in an F1 generation consisting of 120 animals. From this generation, 7 males and 28 females were randomly selected and mated to create an F_2. On average, each female produced 23 female offspring and each male produced 90 female offspring. The total number of female birds in the F_2 generation was 630.

Housing and Management

Birds arrived at the experimental farm as day-old chicks in 5 batches. Every 2 weeks one batch of about 125 animals was delivered (Weeks 30, 32, 34, 36 and 38 in the year 2000). Each batch was allocated at random to two floor pens with an average of 63 birds (between 55 and 70) in each pen, ten pens in total. Each pen measured 4.75 x 2 m and was supplied with wood shavings, two heating lamps per pen for warming and ad libitum feed (152 g/kg crude protein, 2.817 kcal/kg metabolizable energy) and water. From 0 to 4 weeks of age the birds had continuous light (one red heating lamp and two 40 W light tubes per pen). From 5 through 15 weeks of age the heating lamps were removed and the birds had 8 h light between 8:00 and 16:00. From 16 weeks of age onwards, the light period was extended with 1 h per week, until birds had 16 h light between 3:00 and 19:00 at 24 weeks of age. The birds were not beak-trimmed. Each bird was individually marked with a wing tag. Males not excluded from the experiment at 1 d of age, due to errors in gender determination, were removed at 5 weeks of age. At 18 weeks of age, each pen was supplied with laying nests and perches. During the experiment, the mortality rate was 13%, partly because of a coccidiosis infection when the birds were about 20 weeks of age. This infection mostly affected Batches 4 and 5, resulting in more space per bird in these groups. All groups were treated with vitamins and after that treatment no problems with coccidiosis were observed thereafter. The Wageningen University Committee on Animal Care and Use has approved this experiment.

Open-Field Test

At the age of 5 and 29 weeks all birds were tested individually in the open-field test for 10 min. The open-field consisted of a 1.25 x 1.25 m observation pen, which was divided in 25 squares by white markings (5 x 5), measuring 25 x 25 cm each. The front wall was made of Perspex, through which a camera recorded the area of the pen. The observer could then record the behaviour from a video-screen in an adjacent room. General activity and vocalisations were recorded according to the ethogram (Table 6.1).

Table 6.1 Ethogram of the open-field test.

Behaviour	Description
Sitting	Sitting with breast and belly on the floor
Standing	Standing, feet/legs, but not belly on the floor
Walking	Locomotion, minimum of 2 steps
Step	Number of steps
Flying	Flapping wings, no contact with floor
Distress call[1]	Distress call (peep)
Alarm call[2]	Alarm call (kot kot kot kodeeek)
Alarm call note[2]	Alarm call note (kot)
Defecating	Defecating

[1]Only included in the ethogram at 5 weeks of age
[2]Only included in the ethogram at 29 weeks of age

Latencies, durations, and frequencies of all common behaviours were recorded using focal sampling. The catching procedure consisted of entering the homepen, passing a number of birds, walking back to the door, and capturing the first bird in sight, alternating between the two groups of one batch. To avoid unnecessary stress of the individual bird before the test, it was transported to the observation pen in a box. The bird was placed in the middle of the observation pen. The room with the observation pen was dark until the start of the test. At 5 weeks of age, the same person conducted all behavioural observations, but a different experimenter tested and handled Batch 2. At 29 weeks of age two different persons performed the open-field observations, after their behavioural recording methods were brought into conformity with each other. Birds were tested between 8:45 and 16:15. After the test, each bird was marked with a colour across the back (just behind the neck) for identification purposes in the social test. For this purpose 5 different colours (red, green, blue, purple, and orange) were alternated. Earlier observations showed that these colours did not affect feather pecking behaviour or aggressive interactions (T.B. Rodenburg, unpublished data).

Social Test

At 6 and 30 weeks of age all birds were tested in groups of 5 in the social test for 30 min; this test was described previously in Rodenburg and Koene (2001). The social test was executed in the open-field observation pen with wood shavings on the floor. Five birds with different colours were captured from one pen of a batch, alternating between the two pens. They were identified and transported to the observation pen in a crate, where they were placed in darkness. The test began with switching on the light. After 5 min, a sound signal was produced to avoid birds being inactive for 30 min. Body weight of each bird was recorded after the test, and birds were marked with a black dot. One person handled and observed all the birds in the social test. The birds were all tested within the time period 8:45 through 15:45.

Pecking behaviour was sampled directly using behaviour sampling, i.e. sampling all occurrences of some behaviours (Martin and Bateson, 1993). For feather pecking and aggressive pecking both the actor and the receiver were recorded. The ethogram is described in Table 6.2.

Table 6.2 Ethogram of the social test.

Behaviour	Description
Gentle feather peck	Gentle feather peck, no reaction receiver, and neck still
Gentle bout	Bout of gentle feather pecks
Severe feather peck	Severe feather peck, reaction receiver, neck moves
Severe bout	Bout of severe feather pecks
Aggressive peck	Dominance peck, directed at head, neck, or back
Ground bout	Bout of ground pecks. Pecks directed at ground

Statistical Analyses

Exploratory analyses were performed using SAS® (SAS Institute, 1996) by use of the general linear model procedure to estimate sire and dam variances. For the analysis of the open-field test, sire (7 levels) and dam (28 levels; nested within sire) were included in the model as random effects, whereas pen (10 levels), and time of testing (5 levels at 5 weeks and 4 levels at 29 weeks) were included as fixed effects. The social test was analysed with sire (7 levels), and dam (28 levels; nested within sire) included in the model as random effects, and test group (129 levels at 6 weeks and 112 levels at 30 weeks) included as fixed effect. Body weight was analysed in a separate model, including the effects of pen (10 levels) and day (3 levels). Variances were estimated based on information of both sire and dam components of variance. Heritability estimates based on the sire component and the dam component respectively, were then calculated as:

$$h^2_{SIRE} = 4\ \sigma^2_{SIRE}/\sigma^2_P \text{ and } h^2_{DAM} = 4\ \sigma^2_{DAM}/\sigma^2_P.$$

Subsequently an analysis was performed using an animal model and the ASREML software package (Gilmour et al., 2000). Univariate analyses were performed on all recorded traits to estimate the phenotypic and additive genetic variance. For this analysis the following mixed model was used:

$$Y = X\beta + Zu + e$$

where Y is a vector of observations, X is the design matrix for fixed effects, ß is the vector of fixed effects, Z is the design matrix for random effects, u are the random effects with var (u) = $A\sigma^2_u$ and e are the residuals with var (e) = $I\sigma^2_e$. The fixed effects for the open-field test were pen with 10 levels and time of testing with 5 levels at 5 weeks of age and 4 levels at 29 weeks of age. The fixed effect for the social test was test-group with 129 levels at 6 weeks of age and 112 levels at 30 weeks of age. The fixed effects for both tests were the same as used for the exploratory analysis in SAS® (SAS, 1996).

Results

Description of Traits

Means and standard deviations of indicator traits in the open-field test and in the social test at both ages are presented in Table 6.3. In the open-field test at 5 weeks of age, birds on average spent 430 s sitting (72% of total time). If birds became active, they started to vocalise, than they stood up and walked.

Table 6.3 Means and standard deviations of indicator traits in the open-field test at 5 weeks and 29 weeks of age and in the social test at 6 weeks and 30 weeks of age.

Trait	5 weeks		29 weeks	
Open-field test	Mean	SD	Mean	SD
Duration of sitting (s)	431	201	209	252
Duration of standing (s)	134	163	357	241
Latency to first call[1] (s)	334	230	467	191
Latency to stand up (s)	424	205	190	252
Latency to first step (s)	460	184	496	157
Number of steps	30	52	10	25
Number of calls[1]	56	67	34	81
Number of defecations	0.6	1.0	0.7	0.8
Frequency of flying	0.3	0.8	0.03	0.2
Social test	6 weeks		30 weeks	
Number of gentle bouts	0.6	1.3	0.8	1.5
Number of gentle pecks	1.4	3.9	1.5	3.6
Number of severe bouts	0.04	0.29	0.3	0.9
Number of severe pecks	0.09	1.02	0.5	1.5
Number of ground bouts	4.1	5.4	7.3	6.3
Number of aggr. pecks	0.00	0.00	0.14	0.04
Body weight (g)	368	56	1,606	154

[1]Distress call at 5 weeks of age, alarm call at 29 weeks of age

On average, they uttered about 56 distress calls and walked 30 steps. Some birds also tried to fly out of the open-field (mean 0.27 flights per bird). At 29 weeks of age, birds spent less time sitting (35% of total time) and walking (10 steps) and more time standing (60% vs. 22% of total time) than at 5 weeks of age. In the social test, levels of gentle and severe feather pecking and ground pecking were higher at 30 weeks than at 6 weeks of age. Average body weight increased from 368 g at 6 weeks to 1,606 g at 30 weeks. Most distributions of behavioural traits were skewed to the right with many observations with value zero.

Heritabilities

Heritability estimates for open-field behaviours at 5 weeks of age were high (Table 6.4). They ranged from 0.20 for the frequency of flying to 0.49 for number of steps. For number of defecations a h^2 of 0.22 was found. In the social test at 6 weeks of age, only gentle feather pecking (0.12) and ground pecking (0.13) were found to be heritable behavioural traits.

Table 6.4 Heritability (h^2) estimates with standard errors and sire- and dam-based estimates of indicator traits in the open-field test at 5 weeks and in the social test at 6 weeks of age.

Trait	h^2	SE	h^2_{SIRE}	h^2_{DAM}
Open-field test				
Duration of sitting	0.38*	0.12	0.48	0.26
Duration of standing	0.27*	0.11	0.29	0.20
Latency to first call	0.38*	0.13	0.43	0.23
Latency to stand up	0.35*	0.12	0.46	0.22
Latency to first step	0.45*	0.13	0.58	0.29
Number of steps	0.49*	0.13	0.54	0.45
Number of calls	0.32*	0.11	0.61	0.09
Number of defecations	0.22*	0.09	0.32	0.11
Frequency of flying	0.20*	0.09	0.14	0.19
Social test				
Number of gentle bouts	0.12*	0.07	0.21	0.03
Number of gentle pecks	0.08	0.06	0.14	0.00[1]
Number of severe bouts	0.00	0.02	0.00	0.00
Number of severe pecks	0.02	0.04	0.00[1]	0.05
Number of aggr. pecks	0.02	0.03	0.00	0.00
Number of ground bouts	0.13*	0.07	0.21	0.08
Receiving gentle bouts	0.00	0.00	0.00[1]	0.09
Receiving severe bouts	0.00	0.04	0.00	0.00
Receiving aggr. pecks	0.01	0.03	0.00	0.00
Body weight	0.40*	0.13	0.17	0.34

[1] Estimated sire or dam variance component was negative
*h^2 significantly different from zero

Heritability estimates for severe feather pecking and aggressive pecking and for receiving gentle and severe feather pecking and aggressive pecking were not significantly different from zero. For body weight a h^2 of 0.40 was found. When h^2 were estimated based on either sire or dam variances, h^2 estimates based on the dam component of variance were generally lower than those based on the sire component.

At 29 weeks of age, h^2 estimates for behaviours measured in the open-field test were lower than at 5 weeks of age, ranging from 0.10 for duration of sitting to 0.20 for latency to first step (Table 6.5). Heritability estimates of duration of standing, latency to stand up, number of calls, and frequency of flying were not significantly different from zero.

Table 6.5 Heritability (h^2) estimates with standard errors and sire- and dam-based estimates of indicator traits in the open-field test at 29 weeks and in the social test at 30 weeks of age.

Trait	h^2	SE	h^2_{SIRE}	h^2_{DAM}
Open-field test				
Duration of sitting	0.10*	0.06	0.23	0.05
Duration of standing	0.08	0.05	0.23	0.03
Latency to first call	0.18*	0.09	0.43	0.09
Latency to stand up	0.07	0.05	0.11	0.08
Latency to first step	0.20*	0.09	0.28	0.18
Number of steps	0.15*	0.08	0.09	0.21
Number of calls	0.09	0.06	0.19	0.00
Number of defecations	0.16*	0.08	0.22	0.11
Frequency of flying	0.04	0.04	0.03	0.05
Social test				
Number of gentle bouts	0.15*	0.08	0.27	0.14
Number of gentle pecks	0.16*	0.08	0.23	0.19
Number of severe bouts	0.06	0.05	0.07	0.02
Number of severe pecks	0.07	0.05	0.09	0.07
Number of aggr. pecks	0.01	0.03	0.05	0.00[1]
Number of ground bouts	0.30*	0.20	0.28	0.20
Receiving gentle bouts	0.04	0.06	0.00[1]	0.19
Receiving severe bouts	0.00	0.03	0.00	0.00
Receiving aggr. pecks	0.03	0.04	0.06	0.00[1]
Body weight	0.50*	0.14	0.75	0.35

[1] Estimated sire or dam variance component was negative
* h^2 significantly different from zero

In the social test, h^2 were higher compared with 6 weeks of age. For gentle feather pecking bouts a h^2 estimate of 0.15 was found, for gentle pecks an estimate of 0.16, and for ground pecking an estimate of 0.30. Also at 30 weeks of age, h^2 estimates for severe feather pecking and aggressive pecking and for receiving gentle and severe feather pecking and aggressive pecking were not significantly different from zero. Comparable with the results from 5 and 6 weeks of age, h^2 estimates based on the dam component of variance were generally lower than those based on the sire component when h^2 were estimated based on either sire or dam variances.

Discussion

The aim of the current experiment was to estimate h^2 of feather pecking and open-field response in young and adult birds. High h^2 were found for open-field behaviours at 5 weeks of age. In the social test at 6 weeks of age, gentle feather pecking and ground pecking were found to be heritable. At 29 weeks of age, h^2 of open-field behaviours were lower than at 5 weeks of age. For gentle feather pecking and ground pecking higher h^2 were found at 30 weeks of age compared with 6 weeks of age. The h^2 of severe feather pecking was not significantly different from zero at either age.

Heritability Estimates

In the present study h^2 were estimated in an F_2 population. This may affect the estimates, as the variation in the F_1 population is the mean of variation within the original lines (Lande, 1981). If the lines to make the cross would have been inbred strains, the variance between families would be zero. Although inbred strains were not used in the current study, population structure may have affected the estimates. Also the distributions of the traits have to be taken into account. Most distributions of behavioural traits were skewed to the right with many observations with value zero. When h^2 were estimated based on transformed frequencies (square root transformation) and latencies (log transformation), however, estimates were comparable with the estimates based on the non-transformed data, while the distribution of the transformed traits was closer to a relatively normal distribution. Finally, the number of animals used in this experiment was limited compared with studies where h^2 for production traits were estimated. For a behavioural study, however, the current study on 630 individual birds was large and the number of studies on populations of this size is limited. This is mainly due to the labour intensity of behavioural observations at individual level.

Heritabilities Open-Field Test

At 5 weeks of age, h^2 for locomotion traits in the open-field were high. The h^2 of 0.49 for number of steps is in close agreement with the h^2 found by Boyer et al. (1970) for overall movement. The estimated h^2 for number of defecations of 0.22 is higher than those reported by Boyer et al. (1970) and Faure (1981) of 0.06 and 0.10 respectively. At 29 weeks of age, h^2 for open-field behaviours were much lower than at 5 weeks of age, comparable with the results found by Webster and Hurnik (1989) in 17 week old pullets. Most of the open-field tests in poultry have been performed with young chicks (Boyer et al., 1970; Gallup and Suarez, 1980; Faure, 1981; Jones et al., 1995). In chicks, the motivation to return to their flock-mates is strong, as is their fear of being detected by predators. In adult laying hens, these motivations may be less strong, as they seem to be more important to young and vulnerable birds.

Heritabilities Social Test

In the social test at both 6 and 30 weeks of age, only gentle feather pecking, ground pecking, and body weight were found to be heritable traits, with higher h^2 at 30 weeks of age. Kjaer and Sørensen (1997) also found higher h^2 for feather pecking at 38 weeks of age compared with 6 weeks of age. The h^2 estimates for gentle feather pecking of 0.12 at 6 weeks of age and 0.15 at 30 weeks of age fit well with the estimates for total feather pecking in previous studies (Cuthbertson, 1980; Bessei, 1984; Kjaer and Sørensen, 1997). The h^2 of severe feather pecking was not significantly different from zero at both ages. At 6 weeks of age, only 14 out of 630 birds performed severe feather pecking, so the low incidence may be part of the explanation. At 30 weeks of age, however, the incidence was higher and yet the same result was found. This indicates that, under the conditions used in this experiment, the development of severe feather pecking depends mainly on a combination of environmental factors and not so much on genetic factors. In previous studies, no distinction was made between gentle and severe feather pecking, but the present results indicate that it may useful to separate them, as they seem to be controlled by different mechanisms. Heritabilities of receiving gentle or severe feather pecks or aggressive pecks were not significantly different from zero in the present study. In the case of receiving severe feather pecking or aggressive pecking the low incidence may play a role. Kjaer and Sørensen (1997) found a low h^2 (0.15 ± 0.07) for receiving feather pecking at 6 weeks of age.

Sire- and Dam-Based Heritabilities

When h^2 were estimated based on either sire or dam variances, in most cases the sire-based estimates were considerably higher than the dam-based estimates. These results were against expectations, since any presence of dominance and maternal effects would be included in the dam component of variance. Maternal genetic effects have, for instance, been shown to affect body weight and ascites-related traits in broilers (Pakdel et al., 2002). In the present study, the h^2 estimate for body weight based on the dam variance is higher than the estimate based on the sire variance at 6 weeks of age, but lower at 30 weeks of age. The standard errors of the estimates of the sire- and dam-based h^2 were higher than those of the ASREML estimates, which may also explain the apparent differences in sire- and dam-based h^2. Genetic causes may provide an alternative explanation, with possible explanations being sex linkage or parent-of-origin effects. It was not possible to investigate this further from the available data.

In conclusion, gentle feather pecking and open-field response were found to be heritable, which may offer the possibility for genetic selection against feather pecking in the future. For open-field behaviours h^2 were higher at 5 weeks of age compared with 29 weeks of age. For gentle feather pecking, ground pecking and body weight, measured in the social test h^2 were higher at 30 weeks of age than at 6 weeks of age. The h^2 estimate for severe feather pecking was not significantly different from zero at either age. In further research, the relationships between feather pecking and open-field response will be studied to identify possible predictors of feather pecking, supplying tools to select against feather pecking.

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Chapter 7
Genetic and phenotypic correlations between feather pecking and open-field response in laying hens at two different ages

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Abstract

The objective of this study was to estimate genetic parameters of feather pecking and open-field behaviours in laying hens at two different ages. A population of 550 birds of a laying hen cross was subjected to an open-field test at 5 and 29 weeks of age, and to a social feather pecking test at 6 and 30 weeks of age. Factor analysis was used to identify underlying factors for each test: pecking behaviour (social test) and open-field activity (open-field test). Heritabilities of 0.10 at young age and 0.24 at adult age were found for pecking behaviour. For open-field activity, heritabilities of 0.60 at young age and 0.35 at adult age were estimated. At young age, a positive phenotypic correlation of 0.24 was found between high open-field activity and high levels of pecking behaviour. At adult age, a similar genetic correlation of 0.62 was found. Between ages, a strong genetic correlation of -0.65 was found between a high open-field activity at young age and a high level of pecking behaviour at adult age. In conclusion, open-field activity at young age may be used as a predictor of pecking behaviour at adult age.

Introduction

Feather pecking is a behavioural vice that causes welfare- and economic problems in laying hens. Severe feather pecking, the type of feather pecking that causes severe feather damage mostly develops from 18 weeks of age onwards. Once feather pecking has developed in a group of birds, it is very difficult to control. If behavioural characteristics related with feather pecking, and preferably measurable at young age, could be identified, this would provide us with a predictor of feather pecking.

Genetic selection may be an important tool to solve the problem of feather pecking. Selection on feather pecking has been shown to be feasible, using individual selection on feather pecking behaviour (Kjaer et al., 2001). Heritability (h^2) estimates of feather pecking range from 0.07 to 0.56 and for being pecked from 0.00 to 0.15 (Cuthbertson, 1980; Bessei, 1984; Kjaer and Sørensen, 1997).

To reveal the architecture of traits that characterise behaviour in poultry, genetic and phenotypic correlations between traits are needed. This may eventually help to identify possible predictors of damaging feather pecking, which can be used in designing efficient selection strategies. Limited information on correlations is available, however. Kjaer and Sørensen (1997) reported genetic and phenotypic correlations between giving and receiving feather pecks at different ages, based on a population of 310 birds. In their study, phenotypic correlations were generally weak, but genetic correlations between 6, 38 and 69 weeks of age were strong for performing feather pecking. For being pecked, strong genetic correlations were found between the ages of 6 and 69 weeks and the average number of pecks over all ages. Plumage cover had a negative genetic correlation with performing feather pecking, but not with being pecked. Body weight had a negative genetic correlation with performing feather pecking (Kjaer and Sørensen, 1997), whereas Bessei (1984) found positive genetic correlations between feather pecking and body weight.

Feather pecking has been associated with open-field response by Jones et al. (1995). They showed that chicks from a low feather pecking line vocalised and walked sooner in an open-field than chicks from a high feather pecking line. Heritability estimates for open-field behaviours in chicks range from 0.08 to 0.49 for overall locomotion, and from 0.06 to 0.10 for defecation (Boyer et al., 1970; Faure, 1981; Webster and Hurnik, 1989). To date, no information is available on correlations between behaviours measured in the open-field and feather pecking in poultry. Gallup and Suarez (1980) proposed that open-field behaviour in poultry is a compromise between opposing tendencies in a bird to return to its flock-mates and to minimise detection by predators (experimenter). If open-field response at young age is genetically correlated with feather pecking at later age, as the results from Jones et al. (1995) suggested, it may be used as tool in selection against feather pecking.

As mentioned earlier, two types of feather pecking have been distinguished: gentle feather pecking and severe feather pecking (Savory, 1995). Gentle feather pecking can cause some damage but is often ignored by the recipient. Feather pulling, or severe feather pecking, is characterised by forceful pecking at- or pulling out of feathers, to which the victim usually reacts. Feathers that are pulled out are sometimes eaten. It causes feather damage and can lead to bald patches. In a previous paper, h^2 estimates of feather pecking and open-field response at young and adult age were described (Rodenburg et al., 2003). In that study, the heritability estimate for severe feather pecking was not significantly different from zero at either age. Gentle feather pecking (0.12-0.15) and open-field response (0.10-0.49), however, were found to be heritable at both ages.

The aim of the present paper was to study the genetic and phenotypic correlations between feather pecking and open-field response young age, at adult age, and between young and adult age. The latter may help to identify possible predictors of feather pecking at young age, supplying tools to select against feather pecking.

Materials and methods

Genetic Stock and Population Structure

Two selection lines from a commercial breeder were used for this experiment. These lines have been selected for production related traits, but also differ consistently in feather pecking behaviour: the high and low feather pecking lines (Riedstra and Groothuis, 2002; Van Hierden et al., 2002; Rodenburg and Koene, 2003). A reciprocal cross of these lines was made: six high feather pecking males and six low feather pecking females were used to produce the high x low cross and six low feather pecking males and six high feather pecking females were used to produce the low x high cross. This resulted in an F_1 generation consisting of 120 animals. From this generation, seven males and 28 females were randomly selected and mated to create an F_2. On average, each female produced 23 female offspring and each male produced 90 female offspring. The total number of female birds in the F_2 generation was 630. Estimating genetic parameters in an F_2 generation has some disadvantages. These disadvantages were discussed in a previous paper (Rodenburg et al., 2003).

Housing and Management

Birds arrived at the experimental farm as day-old chicks in 5 batches. Every 2 weeks one batch of about 125 animals was delivered (Weeks 30, 32, 34, 36 and 38 in the year 2000). Each batch was allocated at random to two floor pens with an average of 63 birds (between 55 and 70) in each pen, ten pens in total. Each pen measured 4.75 x 2 m and was supplied with wood shavings, two heating lamps per pen for warming and ad libitum feed (152 g kg^{-1} crude protein, 2.817 kcal kg^{-1} metabolizable energy) and water. From 0 to 4 weeks of age the birds had continuous light (one red heating lamp and two 40 W light tubes per pen). At 5 weeks of age the heating lamps were removed and the birds were changed to a light period of 8h between 8:00 and 16:00. From 16 weeks of age onwards, the light period was extended with 1 h per week, until birds had 16 h light between 3:00 and 19:00 at 24 weeks of age. The birds were not beak-trimmed. Each bird was individually marked with a wing tag. Males not excluded from the experiment at 1 day of age, due to errors in gender determination, were removed at 5 weeks of age. At 18 weeks of age, each pen was supplied with laying nests and perches. During the experiment, the mortality rate was 13%, partly because of a coccidiosis infection when the birds were about 20 weeks of age. This infection mostly affected Batch 4 and 5, resulting in more space per bird in these groups. All groups were treated with vitamins and after that treatment no problems with coccidiosis were observed. The Wageningen University Committee on Animal Care and Use has approved this experiment.

Open-Field Test

At the age of 5 and 29 weeks all birds were tested individually in the open-field test for 10 min (Rodenburg et al., 2003). The open-field consisted of a 1.25 x 1.25 m observation pen, which was divided in 25 squares by white markings (5 x 5), measuring 25 x 25 cm each. The front wall was made of Perspex, through which a camera recorded the area of the pen. The observer could then record the behaviour from a video-screen in an adjacent room. General activity and vocalisations were recorded according to the ethogram (Table 7.1).

Table 7.1 Ethogram of the open-field test.

Behaviour	Description
Sitting	Sitting with breast and belly on the floor
Standing	Standing, feet/legs, but not belly on the floor
Walking	Locomotion, minimum of 2 steps
Step	Number of steps
Flying	Flapping wings, no contact with floor
Distress call[1]	Distress call (peep)
Alarm call[2]	Alarm call (kot kot kot kodeeek)
Alarm call note[2]	Alarm call note (kot)
Defecating	Defecating

[1]Only included in the ethogram at 5 weeks of age
[2]Only included in the ethogram at 29 weeks of age

Latencies, durations, and frequencies of all common behaviours were recorded using focal sampling. The catching procedure consisted of entering the homepen, passing a number of birds, walking back to the door, and capturing the first bird in sight, alternating between the two groups of one batch. To avoid unnecessary stress of the individual bird before the test, it was transported to the observation pen in a box. The bird was placed in the middle of the observation pen. The room with the observation pen was dark until the start of the test. At 5 weeks of age, the same person conducted all behavioural observations, but a different experimenter tested and handled Batch 2. At 29 weeks of age two different persons performed the open-field observations, after their behavioural recording methods were brought into conformity with each other. Birds were tested between 8:45 and 16:15. After the test, each bird was marked with a colour across the back (just behind the neck) for identification purposes in the social test. For this purpose 5 different colours (red, green, blue, purple, and orange) were alternated. Earlier observations showed that these colours did not affect feather pecking behaviour or aggressive interactions (T.B. Rodenburg, unpublished data).

Social Test

At 6 and 30 weeks of age all birds were tested in groups of 5 in the social test for 30 min; this test was described previously in Rodenburg and Koene (2003). The social test was executed in the open-field observation pen with wood shavings on the floor. Five birds with different colours were captured from one pen of a batch, alternating between the two pens. They were identified and transported to the observation pen in a crate, where they were placed in darkness. The test began with switching on the light. After 5 min, a sound signal was produced to avoid birds being inactive for 30 min.

Body weight of each bird was recorded after the tests at 6 and at 30 weeks of age, and birds were marked with a black dot. Body weight was recorded because of the suggestion by Kjaer and Sørensen (Kjaer and Sørensen, 1997), that selection on reduced body weight led to increased feather pecking. Furthermore, body weight was used as a reference trait to evaluate the estimated genetic parameters for the behavioural traits. One person handled and observed all the birds in the social test. The birds were all tested within the time period 8:45 through 15:45 h. Pecking behaviour was sampled directly using behaviour sampling, i.e. sampling all occurrences of some behaviours (Martin and Bateson, 1993). For feather pecking and aggressive pecking both the actor and the receiver were recorded. The ethogram is described in Table 7.2.

Table 7.2 Ethogram of the social test.

Behaviour	Description
Gentle feather peck	Gentle feather peck, no reaction receiver, and neck still
Gentle bout	Bout of gentle feather pecks
Severe feather peck	Severe feather peck, reaction receiver, neck moves
Severe bout	Bout of severe feather pecks
Aggressive peck	Dominance peck, directed at head, neck, or back
Ground bout	Bout of ground pecks. Pecks directed at ground

Statistical Analyses

Factor analysis

All traits reported in the previous study (Rodenburg et al., 2003), that had heritability estimates that were significantly different from zero were included in the analysis. Hence, severe feather pecking, aggressive pecking and being pecked were excluded. Because most traits measured in either the open-field test or in the social test were related with each other or mutually exclusive, factor analysis was used to identify underlying factors of the behavioural traits measured in both tests. Because frequencies did not have a normal distribution, they were transformed using a square-root transformation. Latencies were not transformed since the log-transformation had no effect on the distribution. Durations were not included in the factor analysis. Factor analysis (varimax rotation) on frequencies and latencies was done in SAS® (SAS, 1996). For each test, the number of factors was limited to two. In all four tests, factor 1 had a much higher Eigenvalue than factor 2 (2.11 to 7.45 vs. 0.99 to 1.96). Hence, genetic parameters were calculated only for factor 1 of each test. For each bird, factor scores were calculated for each factor and used for further analysis. For each factor heritabilities were estimated, using the method described in Rodenburg et al. (2003).

Genetic analysis

Genetic analysis of the individual traits and the two factor scores was performed using an animal model and the ASREML software package (Gilmour et al., 2000). Bivariate analyses were performed in ASREML on combinations of traits between the two tests and between the two ages to estimate heritabilities and phenotypic and additive genetic correlations. The fixed effects for the open-field test were pen with 10 levels and time of testing with 5 levels at 5 weeks of age and 4 levels at 29 weeks of age. The fixed effect for the social test was test-group, i.e. a group of 5 birds from the same pen and the same batch tested at the same time, with 129 levels at 6 weeks of age and 112 levels at 30 weeks of age.

Results

Factor Analysis

The factors retained from the factor analysis for the open-field test at 5 and 29 weeks of age and the social test at 6 and 30 weeks of age are shown in Table 7.3. Latencies to vocalise, to stand up, and to walk had negative loadings on the factor open-field activity (ACT) at 5 weeks of age, whereas number of steps, calls, and defecations had positive loadings. In the social test at 6 weeks of age, all pecking behaviours (except severe feather pecking and aggressive pecking) and preening had positive loadings on the factor pecking behaviour (PECK). Latencies to walk and to first call had negative loadings on the factor open-field activity at 29 weeks of age, whereas number of steps and calls had positive loadings. Gentle and severe feather pecking, preening and ground pecking showed positive loadings on the factor pecking behaviour at 30 weeks of age.

Table 7.3 Factors retained from the factor analysis for the open-field test (ACT) at 5 and 29 weeks of age and the social test (PECK) at 6 and 30 weeks of age.

Factor	Age (wk)	Var (%)	h^2	SE	Traits contributing most to the factor[1]
ACT	5	47	0.60	0.32	Standing, walking, calling, defecating, flying
PECK	6	41	0.10	0.10	Gentle feather pecking, preening, ground-,wall-pecking
ACT	29	28	0.35	0.21	Calling, walking
PECK	30	35	0.24	0.17	Gentle and severe feather pecking, preening, ground pecking

[1]with a factor loading > 0.50

Open-field activity at young age had a high heritability estimate of 0.60 ± 0.32. At adult age, the estimate was somewhat lower (0.35 ± 0.21). SOC had a low heritability of 0.10 ± 0.10 (NS) at young age and an estimate of 0.22 ± 0.17 (NS) at adult age.

Open-field test and social test at young age

Heritabilities of individual traits were reported previously (Rodenburg et al., 2003), hence here the focus will be on genetic and phenotypic correlations. At 5 weeks of age, both phenotypic and genetic correlations between traits measured in the open-field test were strong (Table 7.4; traits marked with °).

Table 7.4 Heritabilities of (on the diagonal; from Rodenburg et al., 2003), and additive genetic correlations (below the diagonal) and phenotypic correlations (above th diagonal) between traits measured in the open-field test (traits marked^{o}) at 5 wk of age and in the social test (traits marked^{s}) at 6 wk of age.

Trait	Description	Dsit^{o}	Dstand^{o}	Lcall^{o}	Lstan^{o}	Lstep^{o}	Fstep^{o}	Fcall^{o}	Fdefc^{o}	Fgbout^{s}	Fgpck^{s}	Fgrnd^{s}	BW^{s}
Dsit^{o}	Duration of sitting	**0.38**	-0.96*	0.79*	0.97*	0.92*	-0.73*	-0.74*	-0.58*	-0.17*	-0.11*	-0.26*	0.13*
Dstand^{o}	Duration of standing	1.00*,1	**0.27**	-0.76*	-0.94*	-0.85*	0.65*	0.68*	0.51*	0.14	0.08	0.24*	-0.12*
Lcall^{o}	Latency to first call	0.95*	-0.96*	**0.38**	0.79*	0.74*	-0.59*	-0.78*	-0.49*	-0.16*	-0.10*	-0.20*	0.11*
Lstan^{o}	Latency to stand up	1.00*,1	-1.00*,1	0.94*	**0.35**	0.92*	-0.72*	-0.73*	-0.58*	-0.17*	-0.10*	-0.27*	0.14*
Lstep^{o}	Latency to first step	0.99*	-0.99*	0.87*	0.99*	**0.45**	-0.79*	-0.70*	-0.60*	-0.18*	-0.12	-0.27*	0.15*
Fstep^{o}	Number of steps	-0.92*	0.90*	-0.75*	-0.92*	-0.94*	**0.49**	0.50*	0.50*	0.14*	0.10	0.19*	-0.08*
Fcall^{o}	Number of calls	-0.87*	0.86*	-0.89*	-0.88*	-0.85*	0.71*	**0.32**	0.44*	0.19*	0.15	0.21*	-0.16*
Fdefc^{o}	Number of defecations	-0.90*	0.90*	-0.72*	-0.89*	-0.87*	0.99*	0.66*	**0.22**	0.09	0.04	0.18*	-0.01
Fgbout^{s}	Number of gentle bouts	-0.53	0.53	-0.69*	-0.52	-0.56	0.30	0.83*	0.21	**0.12**	0.88*	0.45*	-0.10*
Fgpck^{s}	Number of gentle pecks	-0.33	0.29	-0.52	-0.29	-0.37	0.14	0.70*	-0.13	0.92*	**0.08**	0.35*	-0.08
Fgrnd^{s}	Number of ground bouts	-0.66*	0.64*	-0.59*	-0.69*	-0.65*	0.41*	0.75*	0.46	0.78*	0.45	**0.13**	-0.15*
BW^{s}	Body weight	0.18	-0.14	0.04	0.15	0.31	-0.11	-0.17	0.14	-0.80*	-0.79*	-0.52	**0.40**

*Estimate significantly different from zero, [1]Estimate out of parameter space

In general, genetic correlations were stronger than phenotypic correlations. Strong correlations were found between locomotion traits and number of distress calls; between number of steps and number of calls a genetic correlation of 0.71 ± 0.14 and a phenotypic correlation of 0.50 ± 0.04 was found. In the social test at 6 weeks of age, a positive genetic correlation of 0.78 ± 0.20 was found between gentle feather pecking bouts and ground pecking. A negative genetic correlation was found between body weight and gentle feather pecking (-0.80 ± 0.22; Table 7.4; traits marked [s]). Finally, the factors retained from the factor analysis for the open-field test (open-field activity) and the social test (pecking behaviour) can be used to make a more general comparison of both tests (Table 7.7). A positive phenotypic correlation of 0.24 ± 0.06 was found between open-field activity and pecking behaviour, indicating that birds with a high open-field activity showed much pecking behaviour in the social test. The genetic correlation of 0.55 was stronger, but had a high standard error (0.35; Table 7.7).

Open-field test and social test at adult age

In the open-field test at 29 weeks of age, again correlations between traits were high, with genetic correlations ranging from -1.00 ± 0.01 between latency to first step and number of steps to -0.57 ± 0.34 between latency to first step and number of calls (Table 7.5). Strong phenotypic correlations were found between latency to stand up and duration of sitting (0.96 ± 0.01) and duration of standing (-0.91 ± 0.01). In the social test at 30 weeks of age, none of the genetic correlations was significantly different from zero. Phenotypic correlations were found between gentle feather pecking bouts and pecks of 0.87 ± 0.01 and between ground pecking and gentle feather pecking bouts (0.29 ± 0.04) and pecks (0.28 ± 0.04). The factors retained from the factor analysis were again used to make a further comparison between tests (Table 7.7). A positive correlation of 0.62 ± 0.33 between open-field activity and pecking behaviour, indicating that birds with a high open-field activity showed much pecking behaviour, similar to the correlation found at 5 and 6 weeks of age (Table 7.7).

Table 7.5 Heritabilities of (on the diagonal; from Rodenburg et al., 2003), and additive genetic correlations (below the diagonal) and phenotypic correlations (above th diagonal) between traits measured in the open-field test (traits marked^o) at 29 wk of age and in the social test (traits marked^s) at 30 wk of age.

Trait	**Description**	Dsit^o	Dstand^o	Lcall^o	Lstan^o	Lstep^o	Fstep^o	Fcall^o	Fdefc^o	Fgbout^s	Fgpck^s	Fgrnd^s	BW^s
Dsit^o	Duration of sitting	**0.10**	-0.95*	0.37*	0.96*	0.38*	-0.26*	-0.19*	-0.40*	0.04	-0.03	-0.03	-0.09
Dstand^o	Duration of standing	-0.96*	**0.08**	-0.25*	-0.91*	-0.23*	0.13*	0.13*	0.34*	-0.05	0.02	0.03	0.15*
Lcall^o	Latency to first call	0.67	-0.49	**0.18**	0.34*	0.65*	-0.40*	-0.61	-0.17*	-0.11*	-0.11*	-0.06	-0.14*
Lstan^o	Latency to stand up	1.00*,1	-0.97*	0.75*	**0.07**	0.35*	-0.23*	-0.17*	-0.38*	0.04	-0.02	-0.04	-0.11*
Lstep^o	Latency to first step	0.48	-0.37	0.90*	0.48	**0.20**	-0.63	0.34*	0.46*	-0.05	-0.08	-0.05	-0.17*
Fstep^o	Number of steps	-0.14	0.04	-0.62*	-0.07	-0.98*	**0.15**	0.09*	0.40	0.03	0.04	0.07	0.15*
Fcall^o	Number of calls	-0.72*	0.55	-0.91*	-0.82	-0.57*	0.16	**0.09**	0.09*	0.07	0.22*	0.04	0.09
Fdefc^o	Number of defecations	-0.18	0.14	-0.82*	-0.09	-0.79*	1.00*,1	0.22	**0.16**	0.04	0.08	0.06	0.27*
Fgbout^s	Number of gentle bouts	0.00	0.00	0.00	0.00	0.00	-	0.00	0.00	**0.15**	0.87*	0.29*	-0.04
Fgpck^s	Number of gentle pecks	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.16**	0.28*	0.00
Fgrnd^s	Number of ground bouts	-	-	0.16	-	0.65	-	0.60	-0.73	-	-	**0.30**	0.02
BW^s	Body weight	-0.29	0.37	-0.45	-0.33	-0.45	0.51	0.23	0.67	0.00	0.00	-0.51	**0.50**

*Estimate significantly different from zero, [1]Estimate out of parameter space, - Estimate non-estimable

Correlations between ages

The genetic correlations between traits measured in the open-field test at 5 weeks of age and the social at 6 weeks of age and in the open-field test at 29 weeks of age and the social test at 30 weeks of age are shown in Table 7.6. Duration of sitting in the open-field test at 29 weeks of age was correlated with an active open-field response at 5 weeks of age, with correlations ranging from 0.66 ± 0.31 for duration of standing to 1.00 ± 0.10 for number of defecations. Reversely, duration of standing at 29 weeks of age was correlated with a passive open-field response at 5 weeks of age, with correlations ranging from 0.58 ± 0.34 for duration of sitting to -0.96 ± 0.14 for number of defecations. The latency to first call and the latency to stand up also showed positive correlations with an active open-field response at 5 weeks of age, comparable with the duration of sitting. Furthermore, the number of calls at 29 weeks of age was negatively correlated with the number of steps (-0.62 ± 0.32) and defecations (-0.67 ± 0.30) at 5 weeks of age. None of the genetic correlations between the social test at 6 weeks of age and at 30 weeks of age was found to be significantly different from zero; some were non-estimable.

Table 7.7. Heritabilities of (on the diagonal), and additive genetic correlations (below the diagonal) and phenotypic correlations (above the diagonal) between the factors open-field activity (ACT) and pecking behaviour (PECK) at young$^{(5, 6)}$ and adult age$^{(29, 30)}$.

	ACT^{5}	$PECK^{6}$	ACT^{29}	$PECK^{30}$
ACT^{5}	**0.60***	0.24*	0.04	-0.04
$PECK^{6}$	0.55	**0.10**	0.03	0.04
ACT^{29}	-0.22	0.41	**0.35***	0.15*
$PECK^{30}$	-0.65*	0.33	0.62*	**0.24**

*Estimate significantly different from zero

Between tests, open-field activity at 5 weeks of age was weakly negatively correlated with open-field activity at 29 weeks of age (-0.22; NS; Table 7.7). A high level of pecking behaviour at 6 weeks of age was weakly correlated positively with high open-field activity at 29 weeks of age and a high level of pecking behaviour at 30 weeks of age, but neither correlation was significantly different from zero.

Table 7.6 Genetic correlations between traits measured in the open-field test (traits marked ^{o}) at 5 wk of age and in the social test (traits marked ^{s}) at 6 wk of age and in the open-field test at 29 wk of age and the scoial test at 30 wk of age.

	Open-field test at 29 wk of age and social test at 30 wk of age											
Open-field test at 5 wk of age and social test at 6 wk of age: Trait	Dsit^{o}	Dstand^{o}	Lcall^{o}	Lstan^{o}	Lstep^{o}	Fstep^{o}	Fdefc^{o}	Fcall^{o}	Fgbout^{s}	Fgpck^{s}	Fgrnd^{s}	BW^{s}
Dsit^{o}	-0.72*	0.58*	-0.36	-0.75*	-0.31	0.16	-0.19	0.18	0.00	0.00	-	-0.27
Dstand^{o}	0.66*	-0.52	0.33	0.69*	0.29	-0.13	0.26	-0.12	0.00	0.00	-	0.32
Lcall^{o}	-0.42	0.36	0.06	-0.44	0.16	-0.26	-0.54	-0.17	0.00	0.00	-	-0.39
Lstan^{o}	-0.69*	0.55	-0.38	-0.73*	-0.33	0.17	-0.21	0.19	0.00	0.00	-	-0.30
Lstep^{o}	-0.77*	0.65*	-0.37	-0.79*	-0.38	0.26	-0.06	0.14	0.00	0.00	-	-0.18
Fstep^{o}	0.99*	-0.82*	0.63*	1.00^{*,1}	0.47	-0.21	-0.05	-0.62*	0.00	0.00	-	0.10
Fcall^{o}	0.44	-0.50	0.00	0.47	-0.17	0.25	0.49	0.35	0.00	0.00	-	0.23
Fdefc^{o}	1.00^{*,1}	-0.96*	0.60*	1.00^{*,1}	0.28	0.12	0.22	-0.67*	0.00	-	-	0.03
Fgbout^{s}	0.08	-0.22	-0.50	-0.02	-0.13	-0.25	-0.16	0.88*	0.00	0.00	-	0.00
Fgpck^{s}	-0.22	0.01	-0.77*	-0.33	-0.43	-0.05	-0.11	1.00^{*,1}	0.00	0.00	-	-0.15
Fgrnd^{s}	0.77*	-0.70*	0.16	0.71*	0.38	-0.42	-0.14	0.09	0.00	0.00	-	0.40
BW^{s}	-0.26	0.34	-0.07	-0.17	-0.51	0.89*	0.86*	-0.42	0.00	0.00	-	0.54

*Estimate significantly different from zero, ^{1}Estimate out of parameter space, - Estimate non-estimable.

A strong negative correlation of -0.65 ± 0.31 was found between open-field activity at 5 weeks of age and a high level of pecking behaviour at 30 weeks of age (Table 7.7).

The phenotypic correlations between traits measured in the open-field test and the social test at young and adult age were much lower than the genetic correlations. No phenotypic correlations between the factor scores were significantly different from zero.

Discussion

The aim of the present paper was to estimate the genetic and phenotypic correlations between feather pecking and open-field response at the two different ages. At young age, a positive phenotypic correlation was found between an active open-field response and high levels of pecking in the social test. At adult age, a similar positive genetic correlation between open-field response and pecking behaviour was found. Between ages, a strong negative genetic correlation was found between an active open-field response at young age and a high level of pecking behaviour at adult age.

Estimating genetic parameters

In the present study genetic parameters of behavioural traits were estimated using ASREML. For some traits, heritability estimates were low with large standard errors. This made the estimation of correlations more difficult. In some cases, there were problems with obtaining convergence. This was in some cases solved by changing starting values, while in other cases the variances were standardised by applying rescaling. In all cases the analyses were repeated with different starting values. Also the distributions of the traits have to be taken into account. Most distributions of behavioural traits were skewed to the right with many observations with value zero. In a previous study, however, it was found that estimates based on transformed data were comparable with the non-transformed data, whereas the distribution of the traits was closer to a relatively normal distribution (Rodenburg et al., 2003).

Open-field test and social test at young age

In the open-field test at 5 weeks of age, both phenotypic and genetic correlations between traits were found to be strong. In general, genetic correlations were stronger than phenotypic correlations. Strong correlations were found between locomotion traits and number of distress calls. As described in a previous paper by Rodenburg et al. (2003), birds spent on average 72% of their time sitting. If birds became active, they started to vocalise, than they stood up and walked. Birds were either active (vocalising, walking, defecating) or passive (sitting) in the open-field.

In the social test at 6 weeks of age, a positive genetic correlation was found between gentle feather pecking bouts and ground pecking. As feather pecking has also been described as redirected ground pecking, developed by birds that lacked appropriate substrate for foraging (Blokhuis, 1986) or dustbathing (Vestergaard and Lisborg, 1993), a negative phenotypic correlation may be expected. Gentle feather pecking at early age, however, may also reflect other motivations, such as social exploration (Riedstra and Groothuis, 2002).

At young age, a negative genetic correlation of -0.80 was found between body weight and gentle feather pecking (Table 7.4), which was very similar to the estimate found by Kjaer and Sørensen (1997). Bessei (1984) reported estimates ranging from 0.20 to 0.66 in young birds. Kjaer and Sørensen (1997) reported a negative correlation of -0.62 in adult birds. These results suggested that selection for smaller body size has increased the feather pecking problems in laying hens.

Finally, correlations were found between traits measured in the open-field test and in the social test. Gentle feather pecking was negatively correlated with the duration of sitting and the latency to the first distress call, the latency to stand up, and the latency to the first step. A positive genetic correlation was found between gentle feather pecking and the number of distress calls in the open-field. Gentle feather pecking was also positively correlated with duration of standing, number of steps and frequency of flying. Reversely, Jones et al. (1995) found that chicks from a low feather pecking line vocalised and walked sooner in an open-field than chicks from a high feather pecking line. This difference could be explained by the difference in age of the birds. In a study were birds were tested in an open-field-like test repeatedly at ten different ages, birds from a high feather pecking line vocalised much more than birds from a low feather pecking line at adult age (Rodenburg and Koene, 2003). If this correlation originates from the founder lines, however, a strong genetic correlation would be expected.

Open-field test and social test at adult age

In the open-field test at 29 weeks of age, again correlations between traits were strong. Strong phenotypic correlations were found between latency to stand up and duration of sitting and duration of standing. In the social test at 30 weeks of age, none of the genetic correlations were significantly different from zero. Positive phenotypic correlations were found between gentle feather pecking bouts and pecks and between ground pecking and gentle feather pecking bouts and pecks, comparable with the correlations found at 6 weeks of age. The absence of a negative correlation between ground pecking and gentle feather pecking at adult age indicates that it is not just an effect of age, as suggested earlier. It may be that some birds are genetically predisposed to show more pecking behaviour than other birds in general, irrespective of the form of pecking behaviour.

None of the genetic correlations between the open-field test at 29 weeks of age and the social test at 30 weeks of age were significantly different from zero. Phenotypic correlations were found between number of gentle feather pecks and number of calls and, although weak, between gentle feather pecking bouts and pecks and latency to first call. These correlations were comparable with the phenotypic correlations at young age.

Genetic correlations between ages

A passive open-field response at 5 weeks of age was correlated with an active response at 29 weeks of age and vice versa. Gallup and Suarez (1980) proposed that open-field behaviour in poultry is a compromise between opposing tendencies in a bird to return to its flock-mates and to minimise detection by predators (experimenter). Candland and Nagy (1969) showed that freezing in the open-field reflects fearfulness in chicks. They also found that amount of time spent freezing decreased to nearly zero between 60 and 90 days of age. It may be that activity reflects fearfulness in adult laying hens, as suggested by the correlations found in the present study.

A negative correlation was found between high open-field activity at young age and a high level of pecking behaviour at adult age. Traits contributing most to the factor pecking behaviour at adult age were gentle and severe feather pecking and ground pecking (Table 7.3). Jones et al. (1995) performed an open-field test using chicks from the same high (HFP) and low (LFP) feather pecking lines that were used to breed the cross population used in the present study. They showed that birds from the LFP line vocalised and walked sooner than birds from the HFP line. In adult HFP and LFP birds it was found that HFP birds vocalised much more than LFP birds when tested individually. In HFP birds the level of vocalisations increased with repeated testing, but decreased in LFP birds (Rodenburg and Koene, 2003). The present results from the F2-cross fit well with those results: birds that are inactive in the open-field at young age, are active in the open-field and show a high level of pecking behaviour at adult age, resembling the HFP line. This indicates that early open-field behaviour may be useful as a predictor of later pecking behaviour.

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Chapter 8
General Discussion

Aim and outline

The aim of this thesis was to study the behavioural characteristics of feather pecking in laying hens. A model was proposed on the role of frustration in the development of feather pecking (Chapter 1). In brief, we hypothesised that frustration leads to increased arousal. Increased arousal will result in a stronger pecking motivation. Depending on the availability of a pecking substrate, this results in normal pecking behaviour (with increased intensity) or in redirected pecking behaviour, resulting in feather pecking. The way in which an animal will react to frustration is influenced by its coping strategy, the animal's genetic make up and its environment. In this Chapter, we will discuss our most important results and validate and, when necessary, adjust our model accordingly. Furthermore, we would like to suggest challenging topics for future research and outline possible practical applications of our results.

Importance of the social environment

In Chapter 2, it was shown that feather pecking could best be measured in a social environment and that pecking substrate is indeed important in targeting pecking behaviour. Feather pecking is not comparable with pecking at a bunch of feathers in an individual context (Chapters 2 and 3) or with pecking at feathers fitted at a key of the Skinnerbox (Chapter 4). In a social test, however, both gentle feather pecking and bunch pecking were valid measures of gentle feather pecking in the homepen. These results showed that it is very important to test birds in a social environment and led to the hypothesis that the presence of other birds may play an important role in the development of feather pecking behaviour.

The role of short- and long-term frustration

In the proposed model (Chapter 1), frustration, i.e. the blocking of motivated behaviour, plays a central role in the development of feather pecking. In the experiments, we subjected birds from the high (HFP) and low (LFP) feather pecking lines to frustration in a Skinnerbox. Korte et al. (1997) proposed that these lines have different coping strategies. We hypothesised that these differences in coping strategies might affect the reaction to frustration and, hence, the development of feather pecking. In Chapter 3, we found differences in reaction to frustration, but they were opposite to what we expected. LFP birds reacted stronger to frustration than HFP birds, indicated by key pecking and covered feeder pecking. From the model and the coping strategy hypothesis, one would expect the HFP birds to react stronger to frustration and to show more pecking behaviour. In the discussion of Chapter 3 we argued that HFP birds may have missed an appropriate substrate for pecking, namely feathers or other birds, but in Chapters 4 and 5 we showed that the presence of feathers or other birds made no difference. The main difference in reaction to frustration may be the propensity to redirect pecking behaviour at feathers. This difference may not have been observed in the Skinnerbox experiments because short-term frustration was used. In the individual test used in Chapter 2 evidence was found that birds from the HFP and LFP lines have different ways of coping with repeated testing. HFP birds showed an increase in vocalisations over time, whereas LFP birds showed a decrease. Differences in coping with repeated testing may lead to different propensities to develop feather pecking under long-term frustration. We have not been able to show, however, that short-term frustration can facilitate feather pecking directly in individual birds. In the experiment described by Lindberg and Nicol (1994), birds were frustrated in their homepen over a longer period of time and feather pecking developed in these groups. In Chapter 5, repeated frustration (4 sessions of 15 minutes) was used to see if sensitisation, as seen in Chapter 2, could lead to feather pecking in birds that had not shown feather pecking previous to the experiment. Levels of gentle feather pecking were low, however, and no severe feather pecking developed. From these results we concluded that long-term frustration in a social environment is needed for the development of feather pecking.

Genetics of feather pecking and open-field behaviour

Gentle feather pecking, ground pecking and open-field behaviour were found to be heritable at young age and at adult age. Heritability estimates of severe feather pecking and of being pecked were not significantly different from zero (Chapter 6). Furthermore, non-zero genetic correlations were found between pecking behaviour and open-field response at young and at adult age. We found that a passive open-field response at 5 weeks of age was correlated genetically with a high level of pecking behaviour, including severe feather pecking, at 30 weeks of age (Chapter 7). Jones et al. (1995) performed an open-field test using chicks from the same high (HFP) and low (LFP) feather pecking lines that were used in the present study. They showed that birds from the LFP line vocalised and walked sooner than birds from the HFP line. As there was no difference in tonic immobility response, Jones et al. (1995) argued that LFP chicks had a stronger social motivation. In adult HFP and LFP birds it was found that HFP birds vocalised much more than LFP birds when tested individually. In HFP birds the level of vocalisations increased with repeated testing, but decreased in LFP birds (Rodenburg and Koene, 2003). The present results from the F2-cross fit well with those results: birds that are inactive in the open-field at young age, are active in the open-field and show a high level of pecking behaviour at adult age, resembling the HFP line. This indicates that early open-field behaviour is useful as a predictor of later pecking behaviour.

Gentle and severe feather pecking

In Chapter 1, we stated that gentle and severe feather pecking are not completely clear-cut forms of pecking and may grade into each other, following Savory (1995). Furthermore, McAdie and Keeling (2002) suggested that 'normal' gentle feather pecking, as can be seen at young age, can develop into stereotyped gentle feather pecking or into severe feather pecking by either increased intensity or increased severity of pecking. If that is indeed the case, early gentle feather pecking can be seen as a predictor of later severe feather pecking. Rodenburg et al. (submitted), however, did not find a relationship between gentle feather pecking at early age and severe feather pecking at adult age, whereas gentle and severe feather pecking at the same age were correlated. It was concluded that severe feather pecking may still develop from gentle feather pecking, but whether severe feather pecking develops or not seems to be determined by other, non-genetic factors, such as the social environment and the availability of a suitable substrate for pecking behaviour.

Revising the model

The results presented in this thesis were used to revise the model on the role of frustration in the development of feather pecking in the HFP and LFP lines (Figure 8.1). We hypothesised that HFP birds would react differently to frustration than LFP birds, resulting in higher levels of aggression and fearfulness and a stronger pecking motivation compared with LFP birds. Furthermore, HFP were expected to have a higher propensity to redirect pecking behaviour at feathers, whereas LFP birds were expected to show higher levels of normal pecking. In our experiments, we found that HFP birds indeed showed higher levels of aggression and fearfulness than LFP birds. In our revised model, social motivation and social environment were added, as we found that both play an important role in the development of feather pecking. Birds from the LFP line have a stronger social motivation than HFP birds, as assessed by their open-field activity. Hence, LFP birds are more 'in touch' with their social environment and are less likely to develop high levels of feather pecking. We also found that feather pecking still developed, even when substrates for ground pecking or food pecking were available, especially in birds from the HFP line. It may be that HFP and LFP birds have a different perception of their environment. HFP birds may be more animal-directed in its pecking behaviour and LFP birds more (abiotic) environment-directed (Chapter 2). Finally, we were unable to find direct relationships between feather pecking and coping strategy. A relationship was found between early open-field behaviour and later pecking behaviour, indicating that fearfulness and social motivation affect pecking behaviour, fearful birds with a low social motivation being the birds with the largest propensity to develop feather pecking.

We used the line differences between the HFP and LFP lines, to make a new model on the role of frustration in the development of feather pecking (Figure 8.2). From our experiments we can conclude that short-term frustration in a Skinnerbox does not facilitate feather pecking. Long-term frustration was kept in the model, as Lindberg and Nicol (1994) showed that this can lead to feather pecking.

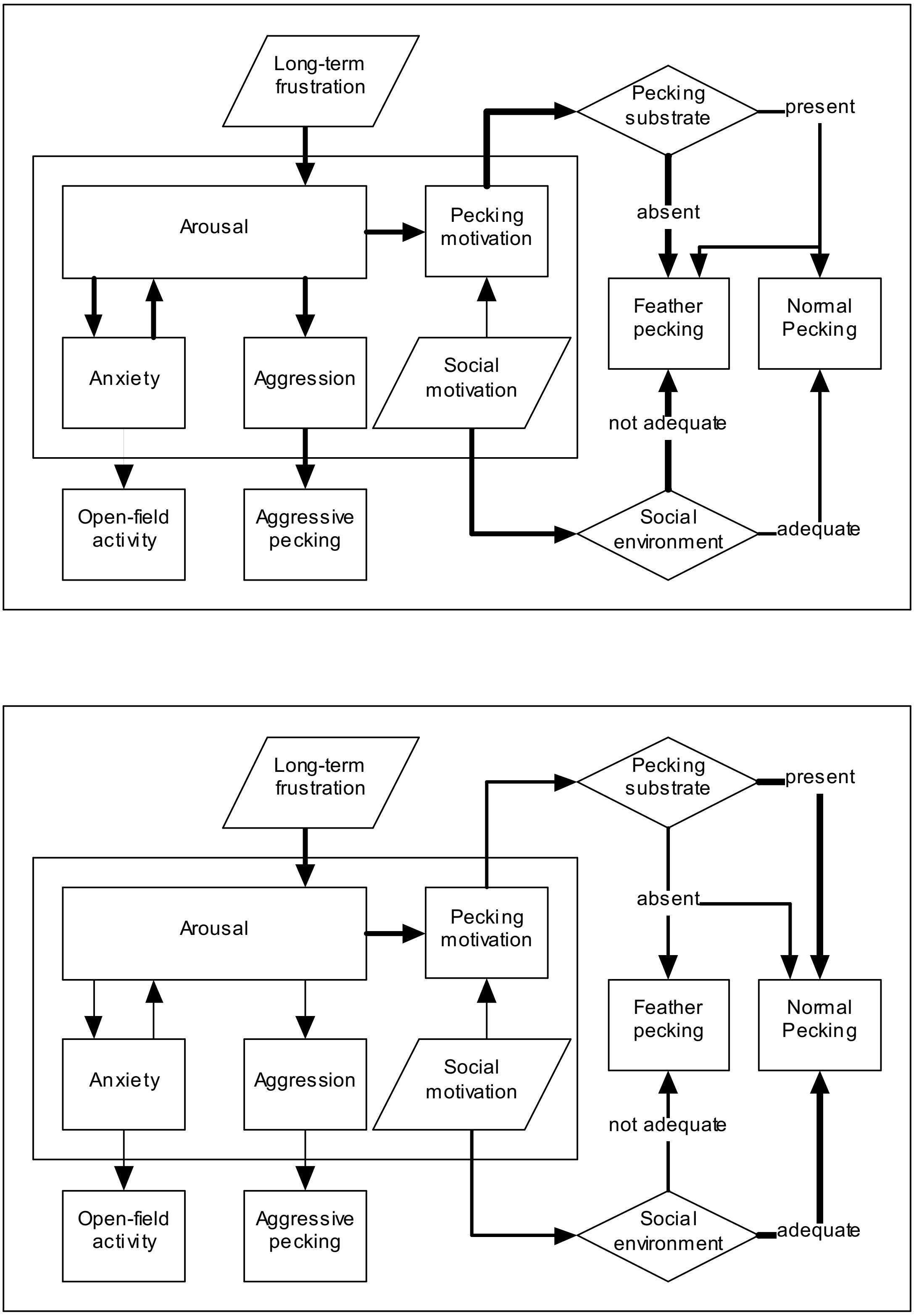

Figure 8.1 The role of frustration in the development of pecking behaviour in the HFP line (top panel) and in the LFP line (bottom panel). Bold arrows represent an increased intensity compared with normal arrows.

Furthermore, the social environment plays an important role in the development of feather pecking. We showed that bunches of feathers or loose feathers in an individual setting are not comparable with feather pecking in a social context. Comparable with the line differences found, feather peckers may have a lower social motivation and less interaction with conspecifics. In combination with a different perception of its environment this may lead to feather pecking.

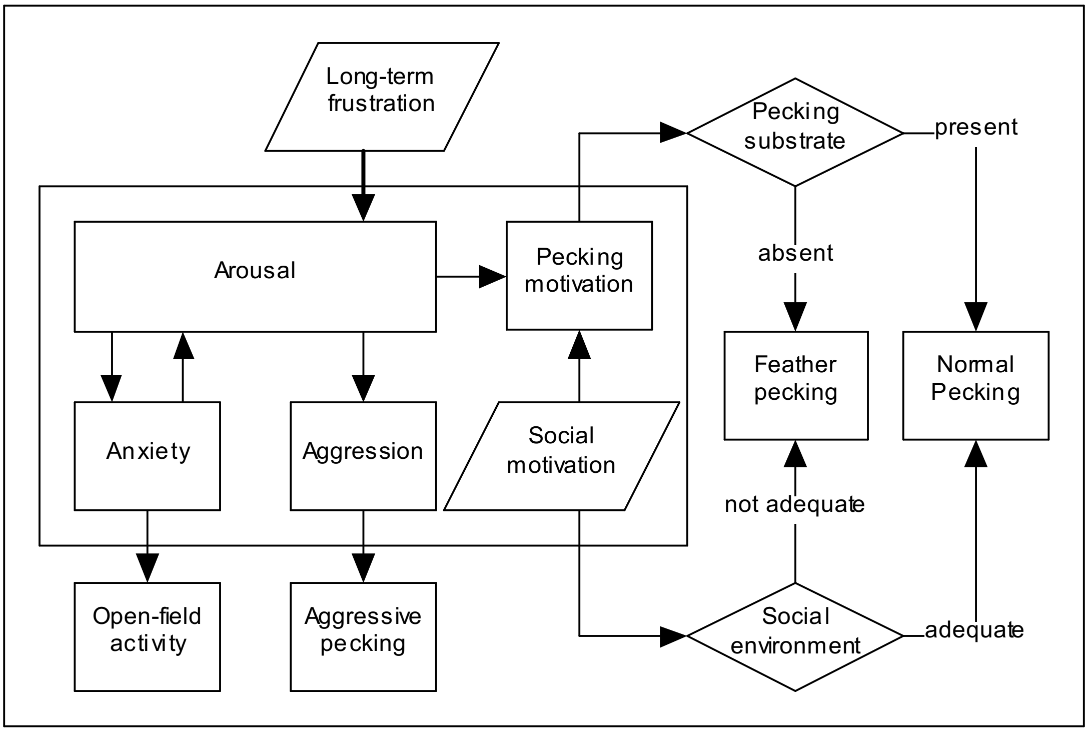

Figure 8.2 Synthesis of the proposed models on the role of frustration in the development of feather pecking and the results from this study.

Relation with abnormal behaviour in other species

The revised model may also be useful in studying abnormal behaviour in other species. Many of the problems we encounter in animals kept in captivity can be related to the availability of substrates or facilities needed and the reaction of an animal when behavioural possibilities are blocked. For instance, many species spent a large amount of time on foraging behaviour in the wild. When animals are kept in captivity, food is provided for the animal. The animal is still motivated to explore, root, peck or chew items in its environment. Hence, bar biting in pigs, tongue playing in veal calves and feather pecking in laying hens all may have a similar background. As mentioned in Chapter 1, feather pecking in laying hens also resembles self-pecking in parrots (Meehan et al., 2003) and tail biting in pigs (Schrøder-Petersen and Simonsen, 2001). Lack of social and environmental stimulation are thought to be important factors in the development of self-pecking in parrots. Similar to feather pecking in laying hens, self-pecking in parrots may be a redirected behaviour, developed because no suitable substrate was available. The major difference between these behaviours is that one is directed to the animal itself and the other to the animal's conspecifics. There is evidence in laying hens, however, that birds that perform much feather pecking, also show high levels of self-preening (Van Hierden et al., 2002; Rodenburg and Koene, 2003), so there may be a relation between the two behaviours. Tail biting in pigs is also regarded as a redirected behaviour (Schrøder-Petersen and Simonsen, 2001). When risk factors that lead to tail biting were explored, availability of straw, solid floors instead of slats and low stocking density were the main husbandry factors reducing the risk of tail biting (Moinard et al., 2003). When a similar study was performed for feather pecking in laying hens, extensive use of the outdoor hen-run, litter availability, and use of bell drinkers were factors that reduced the risk of feather pecking (Green et al., 2000). In both cases, the risk of abnormal behaviour occurring is reduced by space and substrate availability. In a pilot study we housed birds from the HFP and the LFP line on wooden slats, and found that both lines developed high levels of feather pecking. When floor substrate was available, we found that HFP birds showed more feather pecking, whereas LFP birds showed more ground pecking. This shows that under barren conditions all birds develop feather pecking. The main difference between these lines may be found in the perception of environmental stimuli if they are present. Such examples may also be found in other species. This example shows that it is of vital importance to define an appropriate environment if you want to solve behaviour problems in domestic animals, giving an animal enough space and behavioural possibilities to fulfil its behavioural needs.

How to proceed?

In future research, the effects of long-term frustration on the development of feather pecking in groups of laying hens should be studied. In this thesis we showed that birds that differ in feather pecking behaviour also differ in reaction to frustration. Using long-term frustration in a social environment one might be able to show that frustration facilitates the development of feather pecking. By transferring control panels from the individual test environment of the Skinnerbox to the homepen, one could study the effects of frustration in an environment that fits better with current poultry housing systems. Furthermore, it is very important to study the different forms of bird-to-bird pecking behaviour and the relationships between these forms. Our research showed that the different forms are affected differently by genes and environment. Feather pecking, tissue pecking, vent pecking and cannibalism are the main behavioural problems in laying hens. Understanding how these behaviours develop and what the relationships between them are, is the key to control these problems. Finally, behaviour genetics of feather pecking and related characteristics should be studied further, as this seems to be the most promising way to relieve the feather pecking problem. This can help revealing to what extend and in what manner a trait can be changed by breeding schemes.

In practice, poultry farmers can use the information on the relationship between frustration and feather pecking for their own benefit: if sufficient facilities (feeders, drinkers, nests, perches) are available to a flock of birds, frustration can be avoided and the risk of feather pecking reduced. In poultry industry, our tests to measure feather pecking described in Chapter 2 may be useful when studying feather pecking systematically in a commercial population. At the moment, all large breeding companies are developing new breeding strategies and show interest in methods to reduce damaging pecking behaviour (Albers and Van Sambeek, 2002; Besbes, 2002; Preisinger and Schmutz, 2002). For these new strategies, knowledge of the trait feather pecking and how to measure it is fundamental. Heritability estimates and genetic correlations from studies, such as the one described in Chapters 6 and 7, render valuable information on the effectivity of breeding schemes and on the effect of selecting on feather pecking or other traits.

From our results it became clear that the social motivation of a bird and its social environment play an important role in the development of feather pecking. For a social problem, a social selection method is needed. Muir (1996) successfully used group selection to reduce mortality in laying hens. From his experiments, he designed a new selection method, where animals can be selected individually and an adjustment can be made for the effect they have on their group and the effect the group members have on the animal. This method can be used to select birds that fit well in a certain husbandry environment. It is vital to select birds in the environment for which you are breeding birds. Hens that are well adapted to a cage environment, may not be adapted at all to an alternative environment. Before initiating such selection programmes, it is of vital importance to know what traits you should measure. From our results, open-field response at young age and feather pecking behaviour (or plumage condition) at adult age seems measures that can be used.

Furthermore QTL-analysis can tell us whether different traits are affected by the same genes (pleiotropic effects) and which parts of the genome are involved in behavioural traits. The information from the QTL-studies can be used to make genetic selection more effective. QTL studies in laying hens have been performed on fear and foraging behaviour in relation to production traits (Schutz et al., 2002). Furthermore, feather pecking behaviour and stress response (Buitenhuis et al., in press), receiving pecking behaviour (Buitenhuis et al., in prep.-b), and open-field behaviour (Buitenhuis et al., in prep.-a) have been studied. These studies will eventually bring us closer to the genes involved in behavioural traits, supplying improved tools on the longer term for genetic selection against behavioural problems, such as feather pecking.

A question that arises immediately is how far are we prepared to go in adapting the animals to its captive environment? Ali and Cheng (1985) did an experiment with genetically blind chickens. Blind birds layed more eggs than sighted birds and had a higher feed efficiency. They also were less active and had a better feather coverage than sighted birds. This experiment illustrates that is possible to change animals to fit better in our husbandry systems, but where do we draw the line? To most people, creating blind birds is totally unacceptable, yet these birds were still able to eat, drink and lay eggs, although they had no social contact with each other and were less active than sighted birds. On the other hand, taking a bird's eyesight to prevent it from feather pecking is trading one welfare problem for another. Our suggestion would be to first create a suitable environment, providing enough space and facilities to allow birds to fulfil their behavioural requirements. These requirements can be investigated, for example, using preference testing (Elston et al., 2000) and consumer demand studies (Dawkins, 1983). Secondly, when a proper environment has been designed a strain of birds can be selected that fits best in this environment. This can be accomplished by comparing different strains in the same environment, followed by within-line selection. Breeding schemes can be used to breed against undesirable traits, within certain constraints: the ‘end product’ of these breeding schemes should be a bird that has good welfare, good production, an intact body, and that is kept under acceptable housing conditions.

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Summary

Feather pecking in laying hens is characterised by pecking at- and pulling out of feathers of conspecifics. Feather pecking is considered a major welfare- and economic problem. A bird's propensity to develop feather pecking may be related with other behavioural characteristics. The social environment a bird lives in and the bird's social motivation may play an important role in the development of feather pecking. Pecking behaviour can be induced by frustration, i.e. the omission of expected reward. Differences in reaction to frustration may lead to differences in feather pecking. Differences in feather pecking between lines indicate that genetic background plays a role. Studying the behaviour genetics of feather pecking and related behavioural characteristics will improve our understanding of this behaviour and can provide us with valuable tools to select against feather pecking.

The aim of this thesis was to study feather pecking and related behavioural characteristics in laying hens (Chapter 1). To meet this aim, two commercial selection lines were used that differed in feather pecking, the so-called high (HFP) and low (LFP) feather pecking lines. Three research topics were studied:

1. The importance of the social environment: can feather pecking also be studied in individually housed birds by measuring pecking at a bunch of feathers (Chapter 2)?
2. The role of frustration: do feather peckers show a stronger reaction to frustration than non-feather peckers? What is the effect of rearing conditions on feather pecking and reaction to frustration? Does short-term frustration facilitate feather pecking (Chapter 3, 4, and 5)?
3. The behaviour genetics of feather pecking: Are feather pecking and related behavioural characteristics heritable? Can we find a predictor of feather pecking at young age?

In Chapter 2, we aimed to select a suitable test to measure feather pecking in laying hens. Pecking behaviour in individual and social feather pecking tests was compared with pecking behaviour in the homepen for the high (HFP) and low (LFP) feather pecking lines. Six groups of five birds per line were housed on wood shavings with ad libitum food and water. From 7 to 34 weeks of age, every three weeks

pecking behaviour in the homepen was observed and three feather pecking tests were conducted as well: one individual test with a bunch of feathers (10 minutes) and two social tests (in random order), one with and one without a bunch of feathers (30 minutes with whole group). Observations focused on gentle and severe feather pecking, bunch pecking, ground pecking and preening. In the individual test general activity and vocalisations were recorded as well, to measure the response to isolation. In general, HFP birds showed more gentle and severe feather pecking than LFP birds, whereas LFP birds showed more ground pecking and, unexpectedly, more bunch pecking. Birds that showed gentle feather pecking in the homepen also showed gentle feather pecking and bunch pecking in the social tests over all ages. Severe feather pecking in the social test with a bunch of feathers corresponded with severe feather pecking in the homepen. Bunch pecking in the individual test was not a reliable measure for feather pecking in this experiment. An increasing number of vocalisations in the HFP line and a decreasing number in the LFP line indicated a difference in reaction to the individual test. In conclusion, gentle and severe feather pecking and bunch pecking in the social test corresponded best with homepen behaviour, whereas bunch pecking in the individual test did not.

Reaction to frustration of high and low feather pecking laying hens was investigated in Chapter 3, recording pecking behaviour in an automated Skinnerbox. From each of the HFP and LFP lines five feather peckers and five non-feather peckers were selected. Birds with a stronger propensity to develop feather pecking (HFP birds) were also expected to react stronger to frustration, as measured by their pecking behaviour. Birds were trained to peck a key for a food reward in an automated Skinnerbox and subjected to two sessions: a control session, where food was available, and a frustration session, where the feeder was covered with Perspex. These two sessions were repeated in the presence of a bunch of feathers. Unexpectedly, birds from the LFP line had a stronger reaction to frustration than birds from the HFP line, expressed in pecking behaviour. When a bunch of feathers was offered, feather peckers did not show more bunch pecking during frustration than non-feather peckers.

The effect of rearing conditions on feather pecking and reaction to frustration was studied in Chapter 4. From commercial rearing conditions (large group, no mother hen), seven birds from a high feather pecking line (HC birds) and eight birds from a low feather pecking line (LC birds) were used. From semi-natural rearing conditions (small group, mother hen present) seven birds from the high feather pecking line (HN birds) were used. Feather pecking behaviour of HC, LC, and HN groups was recorded for 30 minutes. After that, each bird was food deprived and trained to peck a key for a food reward in a Skinnerbox. After training, each bird was subjected to a frustration session in a Skinnerbox, where the feeder was covered with Perspex. Three HC birds showed severe feather pecking, compared with one HN bird and zero LC birds. Differences in reaction to frustration were found between birds from different lines, but not in birds from different rearing conditions. LC birds tended to put their head in the feeder more frequently than HC birds over all sessions. Although limited, this study indicates that rearing conditions influence feather pecking, but not reaction to frustration.

In Chapter 5, we studied if feather pecking could be facilitated by short-term frustration in birds that had already developed feather pecking prior to the experiment (experiment 1), and in birds that had not (experiment 2). Furthermore, the maximum number of pecks delivered to get access to a food reward was assessed, as birds that deliver a higher maximum number of pecks for a food reward may also react stronger to omission of that reward. We trained birds to peck at a key for a food reward in an automated Skinnerbox and tested them in control and frustration sessions. During frustration, the feeder was covered with Perspex. No evidence was found that feather pecking could be facilitated by short-term frustration in a Skinnerbox, neither in birds that had already developed feather pecking prior to the experiment, nor in birds that had not. However, differences in reaction to frustration and in maximum number of pecks delivered to obtain a food reward between high and low feather pecking birds indicate that frustration may still play a role in the development of feather pecking.

The objective of Chapter 6 was to estimate heritabilities (h^2) of feather pecking and open-field response in laying hens at two different ages. An F_2 cross, originating from a high and a low feather pecking line of laying hens, was used for the experiment. Each of the 630 birds of the F_2 cross was subjected to an open-field test (individual, 10 min) at 5 and 29 weeks of age, and to a social feather pecking test (groups of 5 birds on wood shavings, 30 min) at 6 and 30 weeks of age. Both tests were performed in a square open-field (1.25 x 1.25 m). Behaviour was recorded directly from a monitor. Heritabilities of feather pecking and open-field behaviours were calculated. In the open-field test at 5 weeks of age, high h^2 were found for most traits, ranging from 0.20 for the frequency of flying to 0.49 for number of steps. In the social test at 6 weeks, gentle feather pecking (0.12) and ground pecking (0.13) were found to be heritable. When both tests were repeated at 29 and 30 weeks of age, h^2 estimates were lower for the open-field test, ranging from 0.10 for duration of sitting to 0.20 for latency to first step. In the social test, however, higher h^2 estimates of 0.15 for gentle feather pecking and 0.30 for ground pecking were found compared with 6 weeks of age. In conclusion, gentle feather pecking and open-field behaviours may be used in selection against feather pecking.

To identify a possible predictor of feather pecking, genetic and phenotypic correlations between feather pecking and open-field activity at two different ages were calculated in Chapter 7. These calculations were done on the data of the F_2 cross described in Chapter 6. Factor analysis was used to identify underlying factors for each test: pecking behaviour (social test) and open-field activity (open-field test). At young age, a positive phenotypic correlation of 0.24 was found between high open-field activity and high levels of pecking behaviour. At adult age, a similar genetic correlation of 0.62 was found. Between ages, a strong genetic correlation of -0.65 was found between a high open-field activity at young age and a high level of pecking behaviour at adult age. In conclusion, open-field activity at young age may be used as a predictor of pecking behaviour at adult age.

From our experiments we can conclude that short-term frustration in a Skinnerbox does not facilitate feather pecking. Furthermore, the social environment plays an important role in the development of feather pecking. We showed that bunches of feathers or loose feathers

in an individual setting are not comparable with feather pecking in a social context. Differences in social motivation can explain differences in feather pecking. Birds from the LFP line have a stronger social motivation than HFP birds, as assessed by their open-field activity. Hence, LFP birds are more 'in touch' with their social environment and are less likely to develop high levels of feather pecking. We also found that feather pecking still developed, even when substrates for ground pecking or food pecking were available, especially in birds from the HFP line. It may be that HFP and LFP birds have a different perception of their environment. HFP birds may be more animal-directed in their pecking behaviour and LFP birds more (abiotic) environment-directed (Chapter 2). Finally, we were unable to find direct relationships between feather pecking and coping strategy. A relationship was found between early open-field behaviour and later pecking behaviour, indicating that fearfulness and social motivation affect pecking behaviour, fearful birds with a low social motivation being the birds with the largest propensity to develop feather pecking (Chapter 8). The results found in this study were used to evaluate our model on the role of frustration in the development of feather pecking and a new model was proposed. This knowledge may be used to find a solution for the problem of feather pecking in laying hens.

Samenvatting

Verenpikken, het pikken aan en uittrekken van de veren van soortgenoten, is een belangrijk welzijnsprobleem bij legkippen. De neiging die een kip heeft om aan veren te pikken, zou verband kunnen houden met andere karaktereigenschappen die de kip heeft. De ontwikkeling van verenpikken is ook afhankelijk van de groep waarin de kip leeft en van de interactie van de individuele kip met de groep. Pikgedrag bij kippen kan worden opgewekt door frustratie, het blokkeren van gedrag waarvoor het dier gemotiveerd is. Verschillen in reactie op frustratie kunnen leiden tot verschillen in verenpikken. Verschillen in verenpikken tussen kippenlijnen wijzen erop dat de genetische achtergrond van de dieren een rol speelt. Het bestuderen van de gedragsgenetica van verenpikken en verwante karaktereigenschappen kan ons helpen het probleem beter te begrijpen en kan ons handvaten bieden voor genetische selectie tegen verenpikken.

Het doel van dit proefschrift was het bestuderen van verenpikken en verwante eigenschappen (Hoofdstuk 1). Om dit doel te bereiken, hebben we twee commerciële selectielijnen van legkippen gebruikt, die verschillen in de mate waarin ze verenpikken vertonen: de zogenaamde hoog (HFP) en laag (LFP) verenpikkende lijnen. Het onderzoek heeft zich toegespitst op drie onderwerpen:

1. Het belang van de groep: kan verenpikken ook worden bestudeerd in individueel gehuisveste kippen door pikken op een bosje veren te meten (Hoofdstuk 2)?
2. De rol van frustratie: hebben verenpikkers een sterkere reactie op frustratie dan niet-verenpikkers? Wat is het effect van opgroeicondities op verenpikken en reactie op frustratie? Kan korte frustratie in een Skinnerbox verenpikken opwekken (Hoofdstuk 3, 4, en 5)?
3. De gedragsgenetica van verenpikken: zijn verenpikken en verwante eigenschappen erfelijk bepaald? Kunnen we een voorspeller van verenpikken vinden (Hoofdstuk 6 en 7)?

In Hoofdstuk 2 was het doel om een geschikte test te vinden om verenpikken te meten. Pikgedrag van HFP en LFP dieren in individuele en sociale testen is vergeleken met pikgedrag in het thuishok. Hiertoe zijn zes groepen van 5 dieren per lijn gehuisvest op zaagsel met onbeperkt voer en water. Van zeven tot en met 34 weken leeftijd is elke drie weken het pikgedrag in de thuishok geobserveerd en zijn drie gedragstesten uitgevoerd: een individuele test met een bosje veren (10 minuten) en twee sociale testen, één met en één zonder bosje veren (30 minuten met hele groep). Observaties waren gericht op zacht en hard verenpikken, pikken op het bosje veren, grondpikken en poetsen. In de individuele test zijn ook de activiteit en vocalisaties vastgelegd, om de reactie op isolatie van de groep te bepalen. HFP dieren vertoonden meer zacht en hard verenpikken dan LFP dieren over alle leeftijden heen, terwijl LFP dieren meer grondpikken en, onverwacht, meer pikken op het bosje veren lieten zien. Kippen die zacht verenpikken vertoonden in de thuiskooi, vertoonden ook zacht verenpikken of pikken op het bosje veren in de sociale test. Hard verenpikken in de thuiskooi stemde goed overeen met hard verenpikken in de sociale test. Pikken op het bosje veren in de individuele test bleek geen goede maat te zijn voor verenpikken in de thuiskooi. Verder wees een toenemend aantal vocalisaties in de HFP lijn over de herhaalde testen en een afnemend aantal vocalisaties in de LFP lijn op een verschil in reactie op de herhaalde test.

Reactie op frustratie van verenpikkers en niet-verenpikkers van de HFP en de LFP lijnen is onderzocht in Hoofdstuk 3. Hiertoe zijn van elke lijn vijf verenpikkers en vijf niet-verenpikkers geselecteerd. De verwachting was dat dieren die een sterke neiging tot verenpikken hebben (de HFP dieren), ook sterker reageren op frustratie. Eerst zijn de dieren getraind om op een knop te pikken voor een voerbeloning in de Skinnerbox, daarna zijn ze onderworpen aan twee testsessies: een controle-sessie, waarbij de voerbak gewoon toegankelijk was, en een frustratie-sessie, waarbij de voerbak was afgedekt met een perspex plaatje. Deze twee testsessies zijn herhaald met een bosje veren in de Skinnerbox. Dieren van de LFP lijn bleken, tegen de verwachtingen in, sterker te reageren op frustratie dan dieren van de HFP lijn. Dit kwam tot uitdrukking in hun pikgedrag. Toen een bosje veren werd aangeboden, werd er weinig op gepikt en er was geen verschil tussen verenpikkers en niet-verenpikkers.

In Hoofdstuk 4 is het effect van opgroeicondities op verenpikken en reactie op frustratie bestudeerd in de HFP en LFP lijnen. Van commerciële opgroeicondities (grote groep, geen moederhen) zijn zeven dieren van de HFP lijn (HC dieren) en acht dieren van de LFP lijn (LC dieren) gebruikt. Van semi-natuurlijke opgroeicondities (kleine groep, moederhen aanwezig) zijn zeven dieren van de HFP lijn (HN dieren) gebruikt. De neiging tot verenpikken van de HC, LC en HN groep is gemeten door het pikgedrag gedurende 30 minuten te observeren. Daarna zijn alle dieren gedepriveerd van voer en getraind om te pikken op een knop in een Skinnerbox voor een voerbeloning. Na de training is iedere kip onderworpen aan een frustratie-sessie in de Skinnerbox, waarbij de voerbeloning was afgedekt met Perspex. In de verenpiktest vertoonden drie HC dieren hard verenpikken, tegen één HN dier en nul LC dieren. Verschillen in reactie op frustratie zijn gevonden tussen de lijnen, maar niet tussen dieren van verschillende opgroeicondities. LC dieren staken hun kop vaker in de voerbak tijdens frustratie dan HC dieren over alle sessies heen. Hoewel deze studie een beperkte omvang heeft, wijzen de resultaten erop dat opgroeicondities wel invloed hebben op verenpikken, maar niet op reactie op frustratie.

In Hoofdstuk 5 hebben we gekeken of frustratie op korte termijn kan leiden tot verenpikken. Dit is bekeken bij dieren die al verenpikken vertoonden (experiment 1) en dieren die nog geen verenpikken vertoonden (experiment 2). Ook is het maximum aantal drukken op de knop geregistreerd, omdat kippen die harder willen werken voor een voerbeloning, wellicht ook sterker reageren op het uitblijven van die voerbeloning. Wederom hebben we dieren getraind om op een knop te drukken voor een voerbeloning en getest in controle- en frustratiesessies. Uit de experimenten is niet gebleken dat frustratie op korte termijn kan leiden tot verenpikken in de Skinnerbox, noch in dieren die al verenpikken vertoonden, noch in dieren die nog geen verenpikken vertoonden. Verschillen in reactie op frustratie en in het maximum aantal drukken op de knop voor een voerbeloning tussen verenpikkers en niet verenpikkers wijzen er echter wel op dat frustratie nog steeds een rol kan spelen bij de ontwikkeling van verenpikken.

Het doel van Hoofdstuk 6 was op de erfelijkheidsgraden van verenpikken en open-veldgedrag te schatten op twee verschillende leeftijden. Hiertoe is een F_2 generatie gefokt, afkomstig uit de HFP en LFP lijnen. Ieder dier van de F_2 generatie (n=630) is getest in een open-veld test (individueel, 10 minuten) 5 en 29 weken leeftijd en in een verenpiktest (groep van 5 op zaagsel, 30 minuten) op 6 en 30 weken leeftijd. Beide testen zijn uitgevoerd in een vierkant open-veld (1.25 x 1.25 m). Gedrag is direct geobserveerd via een monitor. Erfelijkheidsgraden van verenpikken en open-veld gedrag zijn geschat. In de open-veld test op 5 weken leeftijd zijn hoge erfelijkheidsgraden gevonden voor de meeste gedragselementen, variërend van 0.20 voor het aantal keren opvliegen tot 0.49 voor het aantal stappen. In de sociale test op 6 weken bleken zacht verenpikken en grondpikken erfelijk te zijn. Toen beide testen herhaald werden op 29 en 30 weken leeftijd, waren de erfelijkheidsgraden voor open-veld gedrag lager dan op 5 weken. In de sociale test, daarentegen waren de erfelijkheidsgraden hoger dan op 6 weken leeftijd, 0.15 voor zacht verenpikken en 0.30 voor grondpikken. Zacht verenpikken en open-veld gedrag zouden bruikbaar kunnen zijn in selectie tegen verenpikken.

Om een mogelijke voorspeller van verenpikken te identificeren, zijn er in Hoofdstuk 7 genetische en fenotypische correlaties berekend tussen verenpikken en open-veld gedrag op jonge en op volwassen leeftijd. Hierbij is gebruik gemaakt van dezelfde dieren en testen als beschreven bij Hoofdstuk 6. Om de onderliggende factoren van iedere test te identificeren is er gebruik gemaakt van factor-analyse. Hiermee is voor iedere test één belangrijke factor geïdentificeerd: pikgedrag (verenpiktest) en open-veld activiteit (open-veld test). Op jonge leeftijd vonden we een positieve fenotypische correlatie (0.24) tussen hoge open-veld activiteit en veel pikgedrag. Op volwassen leeftijd werd een vergelijkbare genetische correlatie gevonden van 0.62. Tussen jonge en volwassen leeftijd vonden we een sterke genetische correlatie van –0.65 tussen hoge open-veld activiteit op jonge leeftijd en veel pikgedrag op volwassen leeftijd. Open-veld gedrag op jonge leeftijd zou dus gebruikt kunnen worden als voorspeller van pikgedrag op volwassen leeftijd.

Uit onze experimenten in de Skinnerbox kan geconcludeerd worden dat frustratie op korte termijn niet leidt tot de ontwikkeling van verenpikken. Verder blijkt de sociale omgeving een belangrijke rol te spelen bij de ontwikkeling van verenpikken. We hebben aangetoond dat pikken op bosjes veren of op veren bevestigd aan een knop in de Skinnerbox niet vergelijkbaar is met verenpikken in een sociale context. Verschillen in sociale motivatie kunnen verschillen in neiging tot verenpikken verklaren. Dieren van de LFP lijn hebben een sterkere sociale motivatie dan HFP dieren. LFP dieren lijken dus meer in verbinding te staan met hun sociale omgeving en hebben een minder sterke neiging tot verenpikken. Verder hebben we gevonden dat verenpikken zich ook ontwikkelde als er wel strooisel aanwezig was om in te foerageren en te stofbaden, vooral bij HFP dieren. Het zou kunnen dat HFP en LFP dieren een verschillende perceptie hebben van hun omgeving. HFP dieren zouden meer dier-gericht kunnen zijn in hun pikgedrag en LFP dieren meer gericht op de abiotische omgeving (Hoofdstuk 2). We hebben geen directe verbanden gevonden tussen verenpikken en coping strategie. Wel is er een relatie gevonden tussen gedrag in het open veld op jonge leeftijd en pikgedrag op volwassen leeftijd, hetgeen erop wijst dat angst en sociale motivatie invloed hebben op pikgedrag. Angstige dieren met een lage sociale motivatie hebben de sterkste neiging tot verenpikken (Hoofdstuk 8). De resultaten die gevonden zijn in deze studie zijn gebruikt om ons model over de rol van frustratie bij de ontwikkeling van verenpikken te evalueren en een nieuw model voor te stellen. Deze kennis zou gebruikt kunnen worden om een oplossing te vinden voor het probleem van verenpikken bij legkippen.

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Curriculum Vitae

Bas (Teunis Bastiaan) Rodenburg werd geboren op 1 april 1975 aan het Lange Voorhout in Den Haag. In 1993 voltooide hij zijn VWO-opleiding aan het Christelijk Gymnasium Sorghvliet in Den Haag. Van 1993 tot en met 1998 studeerde Bas biologie (specialisatie organisme) aan de toenmalige Landbouwuniversiteit Wageningen. In de doctoraalfase specialiseerde hij zich in de toegepaste ethologie, met afstudeervakken op het gebied van verenpikken bij kippen en wroet- en kauwgedrag bij scharrelvarkens. Tijdens zijn stage bij het toenmalige ID-DLO in Lelystad deed Bas onderzoek naar het effect van ruwvoerverstrekking op vleeskalveren. Aansluitend werkte hij daar gedurende 3 maanden als onderzoeksassistent op hetzelfde project. Van 1999 tot 2003 was Bas aangesteld als Onderzoeker in opleiding bij de Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) op het project 'Behavioural characteristics of feather pecking'. Dit project maakte deel uit van het NW0/LNV Prioriteiten Programma 'Grenzen aan welzijn en dierlijke productie' en werd uitgevoerd bij de Leerstoelgroep Ethologie van Wageningen Universiteit onder leiding van dr. Paul Koene. Tijdens zijn promotieonderzoek heeft Bas zich ook ingezet voor het onderwijs (begeleiding afstudeervakken, practica, werkgroepen) en voor de belangen van de promovendi (Aio-raad en WIAS-onderwijscommissie). Sinds 1 mei 2003 is Bas werkzaam als wetenschappelijk onderzoeker bij het Praktijkonderzoek van de Animal Sciences Group van Wageningen UR in Lelystad. Hij is daar betrokken bij onderzoek op gebied van biologische vleeskuikens, legkippen en voeding. Bas woont met zijn vrouw Irene in Heelsum, op een zeer landelijke plek. Hier houden zij enkele schapen en, uiteraard, kippen.

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