

# Neonate pecking preferences and feather pecking in domestic chickens: investigating the ‘changed template’ hypothesis

Pick-Präferenzen und Federpicken bei Hühnerküken: eine Untersuchung der ‘changed template’-Hypothese

J.B. Kjaer

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## Introduction

Feather pecking is a behaviour by which hens destroy the feathers of other hens, in some cases even plucking out feathers and eating these. In some severe cases feather pecking can be followed by cannibalism, where hens eat the blood and tissue of other hens. A wide range of causal factors of feather pecking, such as housing-, rearing-, and feeding factors, have been reported (SHARMA et al., 1999). Furthermore, additive genetic variation is evident (KJAER and SØRENSEN, 1997; RODENBURG et al., 2003), probably determined by one or a few major genes as well as several genes with minor effects (LABOURIAU et al., 2009), meaning that feather pecking is a heritable trait (SU et al., 2005). This fact has made it possible to select lines of laying hens differing in the level of feather pecking (KJAER et al., 2001). Correlated changes of behavioural and physiological traits in these lines (see BUITENHUIS and KJAER, 2008, for an overview) might point to biological mechanisms causing feather pecking to develop in some birds and not in others. Several causal mechanisms have been suggested, the most widely accepted being that feather pecking is a redirection of behaviour related to feeding in the absence of relevant foraging stimuli, the redirected foraging-hypothesis (BLOKHUIS, 1986; DIXON et al., 2008; HOFFMEYER, 1969; HUBER-EICHER and WECHSLER, 1997; LEVY, 1938), but also redirected dust-pecking (VESTERGAARD, 1994; VESTERGAARD and LISBORG, 1993) and redirected social pecking (RIEDSTRA and GROOTHUIS, 2002) have been suggested as possible causal factors in the development of feather pecking. However, these hypotheses of redirected pecking have, with good reason, been challenged (NEWBERRY et al., 2007) and recently it was suggested that a neurologically based hyperactivity-disorder could be triggering the development of feather pecking in some subjects and this could then spread in a group by social facilitation (KJAER, 2009).

None of these hypotheses, though, can give an explanation to the fact that 1) some birds, more than others, change their pecking from normal inanimate targets like feed,

litter and other objects in the environment, to non-normal animate targets like other birds and 2) how individuals’ pecking targets are set (defined) in the first place. There seems to be a kind of innate ‘picture’ (or template) depicting objects, forms, colours or shapes to which chickens are predisposed to peck or to avoid (SUBOSKI and BARTASHUNAS, 1984). These templates are thought to be guidance for the neonatal chicken so pecks are directed in the most effective way in order to gain the necessary food and water and to avoid dangers. Under natural settings, the mother hen will supplement these inherited templates with more explicit information of what to peck by increasing releasing-value of pecked substrates (SUBOSKI, 1984) and thus guide pecking in a certain direction (RIBER et al., 2007; WAUTERS et al., 2002). Could it be that feather pecking evolves in a situation where the templates are wrong and there is no proper guidance from a mother hen as to what targets are ‘right’ and ‘wrong’? Some anecdotal evidence supports this idea. Pheasants are very prone to feather pecking (KJAER, 2004) and neonate pheasant chickens seem to direct more bird-to-bird pecking to pen mates falling over and lying on their back than to pen mates standing on their feet in a normal position (J.B. KJAER, unpublished observations). In domestic laying hens feather pecking seems to be associated with pecking at inanimate objects and it has been suggested that ‘feather pecking may be associated with increased motivation to peck at any object regardless of its nature, or at least when it is presented vertically rather than horizontally’ (CHANNING et al., 1998). Common for these observations is that pecking eliciting properties of certain stimuli depend on physical properties like shape, size and colour and by changing these properties, by for example reversing direction away from ‘normal’, the pecking eliciting properties will also change; i.e. the stimuli will not match the template anymore.

So how can these templates differ between individuals? According to evolution theory one would assume the pecking target templates to have a certain variation between individuals following a normal distribution, and a low inheritance based on a large number of genes (a continuous trait) (FALCONER, 1989). There will be natural selection on these templates, which in a situation with nutritive restrictions (in nature) will keep the development of abnormal templates very rare. Under artificial selection the selection on ‘normal’ templates will be reduced, neutral or even negative in a case where template types are genetically correlated with for example production traits under artificial selection pressure. In the situation with artificial selection for higher (or lower) levels of feather pecking, like in the high and low feather pecking lines used in the present study,

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Institute of Animal Welfare and Animal Husbandry, Friedrich-Loeffler-Institute, Celle, Germany

these templates might even deliberately be changed thus inducing a higher respectively lower level of pecking to objects which not normally would be targets, including feathers of pen mates.

To test this hypothesis of genetically 'changed templates' as a possible causal mechanism of feather pecking behaviour we recorded pecking preferences of young chickens of the high and low feather pecking lines to a range of forms which were presented as pictures on a computer screen. The chicken has a very well-developed visual system and their ability to detect small differences in the sizes and shapes of stimuli, also known as visual acuity, is excellent (Hodos, 1993). Further, there is growing evidence that chickens can process information from televised images and show appropriate responses (CLARKE and JONES, 2000). The seed-shaped circular or ellipsoid forms would possibly indicate feed (templates to peck) whereas more oblong (rods), featherlike objects (rods in a group), or even pictures of a feather, would indicate non feed objects (templates to avoid pecking). Various colours were tested to see if any difference in colour preference could be found between the feather pecking lines. Besides these tests, recording of feather pecking behaviour was made during the first 3 weeks of life. It was expected, according to the 'changed template'-hypothesis, that 1): pecking preferences would differ between lines for forms and more explicitly 2): chickens of the high feather pecking line, compared to chickens from the low feather pecking line, would direct relatively more pecking to the 'feather like' forms and less to the food like forms.

## Methods

### Genetic populations and experimental subjects

A selection experiment was initiated in 1995. A detailed description of the selection procedure is given in KJAER et al. (2001) and SU et al. (2005), and a brief outline is as follows. The founder line was a White Leghorn line formed in 1970 on the basis of a number of commercial lines. Since then this line has been randomly bred. From this population lines have been bred for high (HFP) or low (LFP) levels of feather pecking, respectively. Selection criteria was the individual level of feather pecking recorded from a 3 hour video recording on groups of around 20 individually marked adult (30–40 weeks old) hens. Based on these scores breeding values were calculated using an animal model and thereby including information from relatives. Breeding values of males were calculated on basis of feather pecking of the female relatives. The subjects of the present study were chickens of the 9<sup>th</sup> generation. Feather pecking levels (average (STD)) of adult breeder birds of generation 8 were 7.2 (25.1) and 36.5 (55.3) pecks per bird per hour in the LFP respectively the HFP line.

### Housing and management

A total of 280 chickens were used. They hatched in two batches with 14 days in between. They were sexed at day-old and housed in 20 groups (10 groups of the LFP and 10 groups of the HFP line) of 14 chickens each (7 males and 7 females) in a climate controlled stable (34°C lowered to 20°C during the 5 weeks, 50–80% RH). The pens measured 100 by 100 cm and were fitted with water-nipples and a 1 m long feed trough. Standard chicken feed and water was available *ad libitum*. A layer of 5 cm wood chips covered the floor. Light was supplied from overhead 11 W low energy lamps to a light intensity of 50 to 70 lx. Lighting

program followed the standard program of the Institute, being 24L:0D for the first day, 18L:6D for the next 6 days, 16L:8D for week 2, 14L:10D for week 3, 12L:12D for week 4, 10L:14D for week 5 and 9L:15D for week 6 (end of the experiment).

### Behavioral recordings and variable categorisation

**Screen pecking.** At the age of 15–16 (hatch 1) and 14–15 (hatch 2) days 15 images (Figure 1) showing one of 5 forms (circle, ellipse, rod, rods in feather like pattern, feather) in each of three colours (red, green, yellow) were presented in a random order on a TFT-screen model DT-121-A from DISTRONIC (DISTRONIC, D-65239 Hochheim/Main, Germany). The display was a 12.1" SVGA 600\*800 pixel model LB121S03-TD01 from PHILLIPS (PHILLIPS Deutschland GmbH, D-20001 Hamburg, Germany). A picture (showing one type of form in one colour) was presented for 15 s and a black screen appeared for 2 s between pictures. The collection of pictures was presented for each group of chickens for 25 minutes on each of two days, a total time of 50 minutes. A frame submitting infrared beams in a narrow cross-pattern in front of the display (type IRT 121.V3.0-A251, 12.1" from CITRON GMBH, 86165 Augsburg, Germany) made it possible to automatically record each single peck and these data were stored on hard disk using a custom written computer program.

**Feather pecking.** At the age of 6, 9, and 21 days feather pecking behaviour was recorded with all occurrence sampling by direct observation (ALTMANN, 1973). The observers sat outside the pens and recorded, in good view of, but without disturbing the chickens, all pecking to the feathers of other birds for a period of 10 min for each pen, in total 30 min per pen. Pecks were categorised into 1) gentle, explorative feather pecking, where feathers are not visibly altered in position and 2) severe feather pecking, where the bird grips, pulls or plucks out a feather of another bird, see NEWBERRY et al. (2007) for a more detailed description. A total

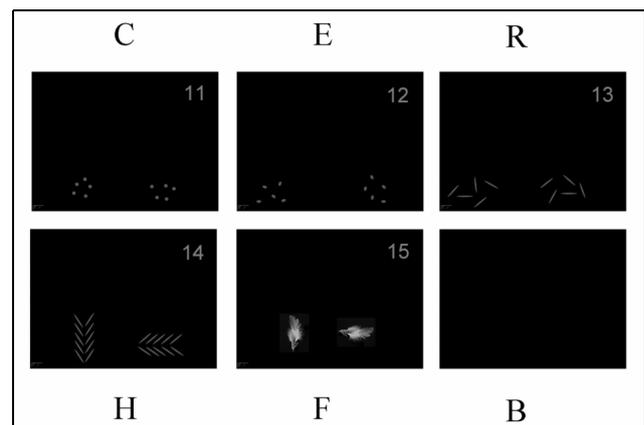


Figure 1. Images showing one of 5 forms (C = circle, E = ellipse, R = rod, H = rods in feather like pattern, F = feather) or the black control screen (B) between pictures. The pictures were presented in red, green or yellow colour and in a random order on a TFT-screen

Die Bilder zeigen eine von fünf Formen (C = Kreis, E = Ellipse, H = Stab in Federform, F = Feder) sowie den schwarzen Bildschirm (B) zwischen den Bildern. Die Bilder wurden in roter, grüner oder gelber Farbe in einer zufälligen Abfolge auf einem TFT-Bildschirm gezeigt.

of 30 minutes of recording was done per pen by three independent observers blind to the treatments. Pen averages (5 pens per line per hatch, in total 20) were used as data points for further analysis. Where nothing else is stated results are presented as pecks per bird per hour.

**Statistical analysis**

Pecking data were analysed by a mixed model with a doubly two dimensional repeated measures model (LITTELL et al., 1996, pp 130–134) using the mixed-procedure of SAS. The model included hatch (1,2), line (LFP, HFP), form (circle (C), ellipse (E), rod (R), feather like pattern (H) and feather (F), see Figure 1), colour (green, red, yellow) and their interactions as fixed factors. Form by pen and colour by pen were included as random factors, assuming that pecking to various forms respectively colours within a pen were correlated. The variance component covariance structure was used. Residuals were found to be normally distributed and least squares means are presented.

Pecks to the black screen shown between pictures as well as data on gentle feather pecking were subjected to analysis of variance using the mixed procedure in SAS with a model including hatch, line and age (6, 9 and 21 days) and their interactions as fixed effects. Age was analysed as a repeated measure, assuming that feather pecking at the three ages was correlated. The variance component covariance structure was used. Residuals were found to be normally distributed and least squares means are presented. Severe feather pecking data was not normally distributed and therefore simple means are presented for this variable and testing was done using a non parametric Wilcoxon Rank Sum test using the NPAR1WAY-procedure of SAS.

**Results**

**Screen pecking**

HFP chickens were found to deliver significantly more pecks than LFP chickens to stimuli on the screen (lsmeans 6.38 vs. 0.97 pecks per bird per hour, mixed model anova  $F_{(1,57.4)} = 64.1, P < 0.001$ ) whereas no effects were found for form ( $F_{(4,48.3)} = 0.65, P > 0.05$ ) and colour ( $F_{(2,28.2)} = 2.94, P > 0.05$ ) or their interactions with line (form\*line-interaction  $F_{(4,48.3)} = 0.21, P > 0.05$ ) (Figure 2). A significant interaction between form and colour was primarily due to a relatively higher difference between pecking to the yellow versus red for ellipse compared to other forms ( $F_{(8,165)} = 2.80, P < 0.01$ ; Figure 3). More pecks were recorded in hatch 2 than in hatch 1 (4.70 vs. 2.64 pecks,  $F_{(1,57.4)} = 6.01, P < 0.05$ ). Only two pecks were given to the black control screen shown between pictures and therefore pecks to the black screen were not further analysed.

**Feather pecking**

Gentle feather pecking did not differ between lines (Mixed Anova, 1.29 vs. 2.04 peck for LFP and HFP lines, respectively,  $F_{(1,56)} = 1.64, P > 0.05$ ) or hatches but decreased with age (2.45, 1.46 and 1.11 pecks at 6, 9 and 21 days of age, respectively,  $F_{(2,56)} = 3.32, P < 0.05$ ). Severe feather pecking was significantly higher in chickens from HFP compared to LFP only at 21 days of age (1.11 vs. 0.49 pecks per bird per hour, Wilcoxon Rank Sum Test,  $Z = 2.0, P < 0.05$ ). Combined (gentle + severe) feather pecking was higher in HFP (Mixed Anova, 3.49 vs. 1.78 pecks,  $F_{(1,56)} = 7.02, P > 0.05$ ) and decreased with age (Mixed Anova, 3.85, 2.44 and 1.61 pecks at 6, 9 and 21 days of age,  $F_{(2,56)} = 4.11, P > 0.05$ ).

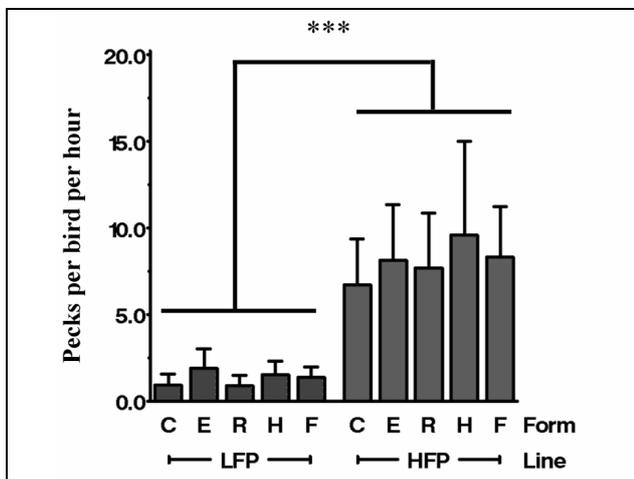


Figure 2. Average level of pecking (N per bird per hour, + 95% C.I.) to a touch screen showing various forms by 14–16 day old chickens from a line selected for less (LFP) or more (HFP) feather pecking. A significant overall effect of line ( $P < 0.001$ , indicated by \*\*\*) was found. Forms did not differ significantly ( $P > 0.05$ ). Forms C = circle, E = ellipse, R = rod, H = rods in a feather like herringbone pattern and F = feather  
*Durchschnittliche Pickhäufigkeit (N je Tier und Stunde, + 95% Konfidenzintervall) bei 14–16 Tage alten Küken von auf geringe (LFP) oder hohe (HFP) Federpickaktivität gezüchteten Linien auf einen Touchscreen, der unterschiedliche Formen zeigte; Es wurde ein signifikanter Linienunterschied gefunden ( $P < 0,001$ , \*\*\*). Die Formen hatten keinen signifikanten Effekt ( $P > 0,05$ ). Form: C = Kreis, E = Ellipse, H = Stab in Federform (Fischgrätmuster), F = Feder*

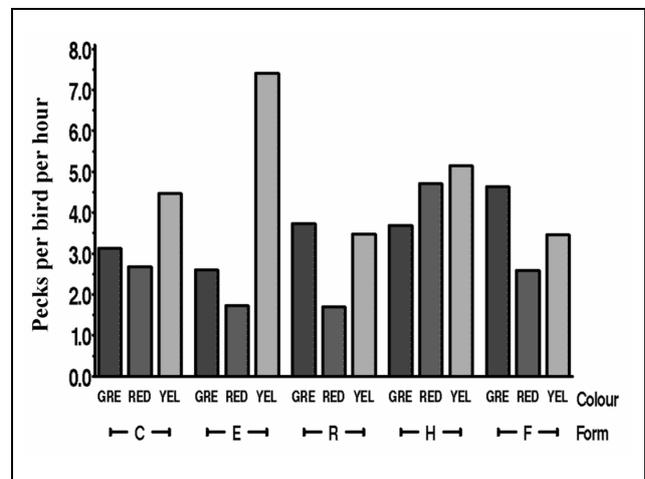


Figure 3. Average level of pecking (N per bird per hour) to a touch screen showing various combinations of forms and colours by 14–16 day old chickens. Combined data from two lines selected for less (LFP) respectively more (HFP) feather pecking was used. Overall interaction between form and colour was significantly different from zero ( $P < 0.01$ ). Forms C = circle, E = ellipse, R = rod, H = rods in a feather like herringbone pattern and F = feather. Colours GRE = green, RED = red and YEL = yellow  
*Durchschnittliche Pickhäufigkeit (N je Tier und Stunde) bei 14–16 Tage alten Küken von auf geringe (LFP) bzw. hohe (HFP) Federpickaktivität gezüchteten Linien (kombinierte Daten) auf einen Touchscreen, der unterschiedliche Formen und Farben zeigte; Die Interaktion zwischen Form und Farbe war signifikant unterschiedlich von Null ( $P < 0,01$ ); Form: C = Kreis, E = Ellipse, H = Stab in Federform (Fischgrätmuster), F = Feder; Farbe: GRE = grün, RED = rot, YEL = gelb*

## Discussion

According to the 'changed template'-hypothesis, HFP chickens would differ from LFP chickens in their pecking preferences to the various forms. This would result in a significant line by form interaction effect. This was, however, not the case and thus the hypothesis could not be supported by the data. One reason for the lack of different preferences could be that the chickens were not able to discriminate between different 2-dimensional forms shown on the computer screen. Chickens are, however, well known to be able to discriminate even subtle differences in two-dimensional pictures (DAWKINS and WOODINGTON, 1997) and there is all reason to believe that chickens indeed were able to discriminate between the various forms and colours shown. Their preference for either of these forms did not differ within or between lines. Two possible explanations can be given for this result. First, visual pecking preferences had not yet developed at this age, at least between the stimuli shown in the present experiment. Alternatively, pecking preferences existed at hatch but the chickens learned, during the 14 days before the experiment, about food and non-food items by explorative pecking and swallowing of 3-dimensional stimuli such as food and litter particles. Testing chickens at an even earlier age would partly overcome this problem.

This leads to the second finding that chickens of the HFP line pecked at any form and colour with a much higher intensity than the LFP chickens. This suggests that feather pecking and general pecking to inanimate objects are genetically correlated traits and do not substitute one another. This result is in contradiction of the redirected foraging hypothesis which rather suggests that feather pecking substitutes general pecking when adequate foraging materials are not available. The recently suggested hyperactivity disorder model of feather pecking states that feather pecking is correlated with an increased, genetically based, general activity (arousal) explaining the significantly higher level of locomotor activity found in chickens from the HFP line at 5 and 13–17 weeks of age (KJAER, 2009). The results found in the present experiment add another element to this model in that also general pecking activity to inanimate objects on a computer screen is higher in the HFP line compared to the LFP line, thereby extending the model to include elevated levels of object pecking as well as elevated levels of locomotor activity.

No effect of colour was evident, but a colour by form interaction was found significant. This was mainly due to relatively high levels of pecking to yellow ellipses and much less to red ellipses. Any biologically meaningful explanation for this result is hard to give but it could be that the yellow ellipse resamples a chicken beak. Beak pecking occurred with approximately the same frequency as gentle feather pecking (around 1 peck per bird per hour) in adult laying hens (STEENFELDT et al., 2007). Colour preferences seem in general to vary much between experiments as they are influenced by a large number of factors such as previous experience, medium and context (JONES and CARMICHAEL, 1998). Bunches of yellow string were found to be pecked more than bunches of orange and blue, but less than white strings by adult laying hens (JONES and CARMICHAEL, 1998). Naive chicks selectively pecked at small, non-green, circular stimuli with regular patterns on the circumference (SUBOSKI and BARTASHUNAS, 1984). The results from the present test, therefore, act more as a guide for further experiments using this method of presentation rather than in formulating general conclusions on colour preferences in young chickens.

Levels of feather pecking (combined) were low but nevertheless significantly higher in the HFP line. Feather peck-

ing was actually not expected to differ at this young age for two reasons. Firstly, because the level of feather pecking is normally low at this age (JENSEN et al., 2006; HUBER-EICHER and WECHSLER, 1997) and secondly, the selection criterion was level of feather pecking in adult hens (at around 30 weeks of age) which seems to be only weakly correlated with feather pecking at a young age (NEWBERRY et al., 2007; RODENBURG et al., 2004). However, those studies were made on phenotypic records within one generation whereas in the present situation genetic selection had taken place over several generations and genetic correlations would therefore seem to be a more appropriate measure. Only two studies on genetic correlations for feather pecking at various ages were found in the literature. Genetic correlation between feather pecking at 6 and 38 weeks of age was found to be 0.87 and significantly different from 0 ( $P < 0.05$ ) whereas the phenotypic correlation in the same study was very low (0.10) and not different from 0 ( $P > 0.05$ ) (KJAER and SØRENSEN, 1997). In a later study, genetic correlation between feather pecking at 6 and 30 weeks of age did not differ from zero (RODENBURG et al., 2003). The lack of correlation in that study, however, could be due to a very low level of feather pecking making the estimation difficult. It should be noted that the level of feather pecking in the present study fell over time (gentle feather pecking was 2.45, 1.46 and 1.11 pecks at 6, 9 and 21 days of age), indicating that the level at 6 weeks of age might be even lower. Indeed, recordings done at 5 weeks of age in a separate study and presented elsewhere (KJAER, 2009) showed very low levels of gentle feather pecking (0.44 pecks on average for LFP and HFP chickens) and even less severe feather pecking, on average 0.07 pecks per bird per hour. Such low levels would definitively lead to low genetic correlations like in the study of RODENBURG et al. (2003). Fortunately the methodology used in the present study, using divergently selected lines, overcomes the problem of low intra-generation correlations by aggregating effects over several generations of selection. It is therefore superior to the 'one generation' methodology in finding traits being genetically connected but still highly influenced by age and environmental causes.

In conclusion, the 'changed template'-hypothesis suggesting that feather pecking is arising in chickens with an inherited preference for pecking motives different to that of non feather pecking, naïve, young chickens, could not be supported by results from the present study. Rather, the results lend support to the hyperactivity model of feather pecking in that genetic selection for a higher levels of feather pecking is paralleled by a higher level of arousal, leading to higher locomotor activity, and higher levels of pecking to animate (other animals) as well as inanimate (i.e. forms on a screen) stimuli.

## Summary

Domestic chickens from lines selected for low (LFP) or high (HFP) levels of feather pecking (FP) were reared in 14 bird groups and pecking to various forms presented on a computer screen was recorded at 2 weeks of age. HFP chickens delivered significantly more pecks (combined for all forms: circle, ellipse, rod, rods in feather like pattern and feather in colours: red, yellow, green) than LFP chickens, whereas no significant effects were found for form, colour, hatch or interactions. Total FP (sum of gentle and severe FP) was significantly higher in HFP chickens and decreased significantly with increasing age from 6 over 9 to 21 days. According to the 'changed template'-hypothesis, pecking preferences of HFP chickens would differ to those

of LFP chickens but data could not support this hypothesis. Rather, the HFP chickens pecked at any form and colour with a much higher intensity than the LFP chickens lending support to the hyperactivity model of feather pecking in that genetic selection for a higher level of FP is paralleled by a higher level of arousal leading to increased pecking to animate (FP) as well as inanimate (i.e. forms on a screen) stimuli.

### Key words

Laying hen, genetic selection, hyper activity model, inherited templates, neonate feather pecking, pecking preferences

### Zusammenfassung

#### Pick-Präferenzen und Federpicken bei Hühnerküken: eine Untersuchung der 'changed template'-Hypothese

Haushühner aus zwei Zuchtlinien, die auf geringes (LFP) und hohes (HFP) Federpicken (FP) gezüchtet wurden, wurden in Gruppen von 14 Tieren aufgezogen. Das Picken nach verschiedenen Formen, die auf einem Computer-Bildschirm angezeigt wurden, wurde im Alter von 2 Wochen erfasst. Die HFP Küken pickten signifikant mehr (Kombination aller Formen: Kreis, Ellipse, Stab, Stab in Federform, Federn in den Farben rot, gelb, grün) als die LFP Küken. Allerdings konnten keine signifikanten Effekte der Behandlungsfaktoren Form, Farbe, Schlupf oder deren Interaktionen festgestellt werden. Die gesamte Pickaktivität (Summe von leichtem und starkem Picken), die im Alter von 6, 9 und 21 Tagen ermittelt wurde, war bei den HFP Küken signifikant am höchsten und nahm mit dem Alter ab. Nach der 'changed template' Hypothese müssten sich die Pickpräferenzen der HFP Küken von denen der LFP Küken unterscheiden. Dies konnte allerdings nicht beobachtet werden, so dass die Daten diese Hypothese nicht bestätigen. Nachdem die HFP Küken generell nach allen Formen und Farben viel häufiger pickten als die LFP Küken scheint eher die Hyperaktivitätshypothese zu zutreffen. Die genetische Selektion auf eine höhere Federpickaktivität scheint mit einem erhöhten Erregungslevel einherzugehen, der sich in einer erhöhten Pickaktivität sowohl gegen lebende (Federpicken) als auch gegen leblose (z.B., Formen auf einem Bildschirm) Stimuli äußert.

### Stichworte

Legehennen, genetische Selektion, Hyperaktivitätsmodell, vererbte Schablone, Picken des Kükens, Pickpräferenzen

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### References

- ALTMANN, J., 1973: Observational study of behaviour: sampling methods. *Behav.* **49**, 227-267.
- BLOKHUIS, H.J., 1986: Feather-pecking in poultry: its relation with ground-pecking. *Appl. Anim. Behav. Sci.* **16**, 63-67.
- BUITENHUIS, A.J., J.B. KJAER, 2008: Long term selection for reduced or increased pecking behaviour in laying hens. *Worlds Poult. Sci. J.* **64**, 477-487.
- CHANNING, C.E., P.M. HOCKING, R.B. JONES, 1998: Feather pecking in adult laying hens: can it be associated with pecking at inanimate objects? *Br. Poult. Sci.* **39**(Suppl S), S15-S16.
- CLARKE, C.H., R.B. JONES, 2000: Responses of adult laying hens to abstract video images presented repeatedly outside the home cage. *Appl. Anim. Behav. Sci.* **67**, 97-110.
- DAWKINS, M.S., A. WOODINGTON, 1997: Distance and the presentation of visual stimuli to birds. *Anim. Behav.* **54**, 1019-1025.
- DIXON, L.M., I.J.H. DUNCAN, G.J. MASON, 2008: What's in a peck? Using 'fixed action pattern' morphology to investigate the motivational basis of feather pecking in laying hens. *Anim. Behav.* **76**, 1035-1042.
- FALCONER, D.S., 1989: Introduction to quantitative genetics. Essex, England, Longman Scientific and Technical, ISBN 0-582-016428.
- HODOS, W., 1993: The visual capabilities of birds. In Zeigler, H.P. and Bischof, H.-J. (eds) *Vision, Brain and Behaviour in Birds*. The MIT Press, London, England, 63-76.
- HOFFMEYER, I., 1969: Feather pecking in pheasants – an ethological approach to the problem. *Danish Rev. Game Biol.* **6**, 1-36.
- HUBER-EICHER, B., B. WECHSLER, 1997: Feather pecking in domestic chicks: its relation to dustbathing and foraging. *Anim. Behav.* **54**, 757-768.
- JENSEN, A.B., R. PALME, B. FORKMAN, 2006: Effect of brooders on feather pecking and cannibalism in domestic fowl (*Gallus gallus domesticus*). *Appl. Anim. Behav. Sci.* **99**, 287-300.
- JONES, R.B., N.L. CARMICHAEL, 1998: Pecking at string by individually caged, adult laying hens: colour preferences and their stability. *Appl. Anim. Behav. Sci.* **60**, 11-23.
- KJAER, J.B., 2004: Effect of stocking density and group size on feather and skin condition of the skin and feathers of pheasant chicks. *Vet. Rec.* **154**, 556-558.
- KJAER, J.B., 2009: Feather pecking in domestic fowl is genetically related to locomotor activity levels: Implications for a hyperactivity disorder model of feather pecking. *Behav. Gen.* **39**, 564-570.
- KJAER, J.B., P. SØRENSEN, 1997: Feather pecking behaviour in white leghorns – a genetic study. *Br. Poult. Sci.* **38**, 333-341.
- KJAER, J.B., P. SØRENSEN, G. SU, 2001: Divergent selection of feather pecking behaviour in laying hens (*Gallus gallus domesticus*). *Appl. Anim. Behav. Sci.* **71**, 229-239.
- LABOURIAU, R., J.B. KJAER, G. ABREU, J. HEDEGAARD, A.J. BUITENHUIS, 2009: Analysis of Severe Feather Pecking Behavior in a High Feather Pecking Selection Line. *Poult. Sci.* **88**, 2052-2062.
- LEVY, D.M., 1938: On instinct-satiation: an experiment on the pecking behaviour of chickens. *J. Gen. Psychol.* **18**, 327-348.
- NEWBERRY, R.C., L.J. KEELING, I. ESTEVEZ, B. BILCIK, 2007: Behaviour when young as a predictor of severe feather pecking in adult laying hens: The redirected foraging hypothesis revisited. *Appl. Anim. Behav. Sci.* **107**, 262-274.

- RIBER, A.B., A. WICHMAN, B.O. BRAASTAD, B. FORKMAN, 2007: Effects of broody hens on perch use, ground pecking, feather pecking and cannibalism in domestic fowl (*Gallus gallus domesticus*). *Appl. Anim. Behav. Sci.* **106**, 39-51.
- RIEDSTRA, B., T.G.G. GROOTHUIS, 2002: Early feather pecking as a form of social exploration: the effect of group stability on feather pecking and tonic immobility in domestic chicks. *Appl. Anim. Behav. Sci.* **77**, 127-138.
- RODENBURG, T.B., A.J. BUITENHUIS, B. ASK, K.A. UITDEHAAG, P. KOENE, J.J. VAN DER POEL, H. BOVENHUIS, 2003: Heritability of feather pecking and open-field response in laying hens at two different ages. *Poult. Sci.* **82**, 861-867.
- RODENBURG, T.B., Y.M. VAN HIERDEN, A.J. BUITENHUIS, B. RIEDSTRA, P. KOENE, S.M. KORTE, J.J. VAN DER POEL, T.G.G. GROOTHUIS, H.J. BLOKHUIS, 2004: Feather pecking in laying hens: new insights and directions for research? *Appl. Anim. Behav. Sci.* **86**, 291-298.
- SHARMA, V., D. CHAND, D.V. ARNEJA, 1999: Feather pecking and cannibalism in poultry: causes and control measures. *Int. J. Anim. Sci.* **14**, 117-121.
- SU, G., J.B. KJAER, P. SØRENSEN, 2005: Variance components and selection response for feather-pecking behavior in laying hens. *Poult. Sci.* **84**, 14-21.
- STEENFELDT, S., J.B. KJAER, R.M. ENGBERG, 2007: Effect of feeding silages or carrots as supplements to laying hens on production performance, nutrient digestibility, gut structure, gut microflora and feather pecking behaviour. *Br. Poult. Sci.* **48**, 454-468.
- SUBOSKI, M.D., 1984: Stimulus configuration and valence-enhanced pecking by neonatal chicks. *Learning and Motivation* **15**, 118-126.
- SUBOSKI, M.D., G. BARTASHUNAS, 1984: Mechanisms for social transmission of pecking preferences to neonatal chicks. *J. Exp. Psychol.* **10**, 182-194.
- VESTERGAARD, K.S., 1994: Dustbathing and its relation to feather pecking in the fowl: Motivational and developmental aspects. Dissertation, The Royal Veterinary and Agricultural University, Copenhagen. Jordbrugsforlaget, DK-2000 Frederiksberg.
- VESTERGAARD, K.S., L. LISBORG, 1993: A model of feather pecking development which relates to dustbathing in the fowl. *Behav.* **126**, 291-308.
- WAUTERS, A.-M., M.-A. RICHARD-YRIS, N. TALEC, 2002: Maternal influences on feeding and general activity in domestic chicks. *Ethol.* **108**, 529-540.

Correspondence: Dr. J.B. Kjaer, Institute of Animal Welfare and Animal Husbandry, Friedrich-Loeffler-Institute, Dörnbergstr. 25-27, 29223 Celle, Germany; e-mail: joergen.kjaer@fli.bund.de