

Influence of Rearing Environment on Development of Perching and Dustbathing Behaviour in Laying Hens

Anette Wichman

*Faculty of Veterinary Medicine and Animal Science
Department of Animal Environment and Health
Skara*

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Abstract

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Studies have shown that perching and dustbathing behaviour in birds can be affected by how and when the behaviour develops. With the increasing trend away from cages and towards keeping laying hens in larger, more complex housing systems, it is important to improve our knowledge about what chicks need to learn if they are going to be able to fully use perches and litter when these are provided to them as adults.

In the first part of this thesis the early use of perches and how this was influenced by the bird's behaviour during the first weeks of life was investigated at the individual level. Furthermore the relationship between a bird's spatial ability as a chick and as an adult was investigated by testing birds in two different two-dimensional spatial tests and by observing their use of perches. The aim was to investigate the degree to which birds are hatched with spatial skills or acquire these by using perches. The second part of the thesis dealt with the importance of access to an appropriate, that is to say, functional substrate for the development of dustbathing behaviour. Here comparisons of dustbathing behaviour by birds with different experiences of peat, a preferred dustbathing substrate, were carried out. In addition it was investigated whether birds that had only ever known sham dustbathing would be as motivated to get access to peat for dustbathing as birds reared and used to performing functional dustbathing.

It was found that behaviour, such as spending more time underneath the perches, related positively with early perch use and the ability to solve a two dimensional spatial test was related to use of perches in a novel situation as adult. However, the results did not shed any light on whether chicks hatched with good spatial ability or if the spatial ability mostly developed through the use of perches. Dustbathing behaviour was influenced mainly by the substrate and the birds which gained or lost access to peat changed their dustbathing behaviour according to if they dustbathed in peat or on paper. Birds dustbathing on paper performed a less coherent dustbathing behaviour with more long and short bouts than birds dustbathing on peat. Irrespective of treatment all birds were motivated to get access to peat for dustbathing. These results imply that sham dustbathing can not replace functional dustbathing for a hen. In combination, the results of this thesis confirm the importance of giving early access to litter and perches also to the young chick.

Keywords: domestic chicken, dustbathing, *Gallus gallus domesticus*, ontogeny, perching, rearing, spatial ability.

Author's address: Anette Wichman, Department of Animal Environment and Health, Swedish University of Agricultural Sciences, P.O. Box 234, SE-532 23 Skara, Sweden,
E-mail: Anette.Wichman@hnh.slu.se

Contents

Introduction, 7

- Commercial egg production, 7
- Natural behaviour, 7
- Motivation and animal welfare, 8
- Factors affecting bird welfare in commercial systems, 10
- Ontogeny, 11
- Development of perching, 12
- Development of dustbathing, 13

Aims of thesis, 15

Material and methods, 15

- Animals, 15
- Housing, observations and test methods, 16
 - Papers I and II, 16*
 - Papers III and IV, 18*
- Statistical analyses, 20

Summary of results, 21

- Paper I, 21
- Paper II, 21
- Paper III, 21
- Paper IV, 22

General discussion, 23

- Development of perching behaviour, 23
 - Behaviours related to start of perching, 23*
 - Day time and night time perching, 24*
 - Effects of enrichment on perching, 24*
 - Spatial ability and perching, 25*
- Development of dustbathing behaviour, 26
 - Effects of access to peat during rearing on dustbathing behaviour, 26*
 - Do birds have a need to dustbathe in litter? 28*
- Comparison of development of perching and dustbathing, 29
 - Importance of access to resources, 29*
 - Is it possible to miss something one has never experienced? 29*
- Methodological considerations, 30
 - Spatial tests and perching observations, 30*
 - Treatments and observations of dustbathing behaviour, 31*
 - Push-door, 32*

Conclusions, 33

Svensk sammanfattning, 34

References, 37

Acknowledgements, 42

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Heikkilä, M., Wichman, A., Gunnarsson, S. & Valros, A. 2006. Development of perching behaviour in chicks reared in enriched environment. *Applied Animal Behaviour Science* 99, 145-156.
- II. Wichman, A., Heikkilä, M., Valros, A., Forkman, B. & Keeling, L. J. 2007. Perching behaviour in chickens and its relation to spatial ability. *Applied Animal Behaviour Science* 105, 165-179.
- III. Wichman, A. & Keeling, L. J. The influence of losing or gaining access to peat on the dustbathing behaviour of domestic chickens. *Manuscript*.
- IV. Wichman, A. & Keeling, L. J. Hens are motivated to dustbathe in peat irrespective of being reared with or without a suitable substrate. *Submitted*.

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Introduction

Commercial egg production

The domestic chicken is used to produce food for human consumption and in Sweden alone 6 million laying hens are kept for egg production. During the industrialization of the last century the way chickens were housed changed from keeping a flock in the backyard to large commercial production systems housing thousands of birds. Cages were developed which made care taking and egg collection easy and provided a relatively parasite free environment. In addition, the possibility to keep birds in small groups led to fewer birds becoming victims if some birds began to feather peck or cannibalize the other hens. However, the welfare of food producing animals has become a topic of concern during the last decades because of the barren conditions these animals are often housed under. Such housing conditions leave little opportunity for the animals to perform behaviours which should be a natural part of their behavioural repertoire. Laying hens in conventional cages attracted much attention in this debate and the concerns resulted in a decision to ban the conventional cage from 1999 in Sweden (SFS, 1988) and from 2012 they will be banned also in EU (CEC, 1999). Instead of conventional cages laying hens should be housed in different types of loose-housing systems or in modified cages where access to perches, nest boxes and dustbathing material has to be provided.

In conventional cages the floor is made of wire netting and the only resources provided are water and food. The area in each cage is small and before the cages were banned in Sweden it was allowed to keep three laying hens per cage. The modified or furnished cages, as they are also called, are larger and house around eight birds per cage although the exact number of birds and layout varies between cage types. In these cages the floor is of wire but they also contain a perch, a nest and a litter bath. There are several different types of loose-housing systems in use in commercial egg production. Most of these can house several thousand birds in the same section. The design of the house varies from floor systems to systems with several tiers. Litter is provided on the floor and perches can be placed at several different heights and often food, water and nest boxes are placed above ground so that the bird has to use the tiers to find these resources. Laying hen chicks are usually reared on one farm and moved to the laying facilities on a different farm a few weeks prior to onset of lay. This can lead to birds being reared in a different housing system to the one they will be kept in as adults. After having moved to the laying facilities birds remain there until slaughtered. Birds are slaughtered when they are around 70-80 weeks and their production rates have decreased.

Natural behaviour

The red junglefowl is believed to be the ancestor of the domestic chicken and studies of feral fowl have shown their behaviour to be similar to the junglefowl (McBride, Parer & Foenander, 1969). Free living chickens form small social

groups and spend a large part of their active time, mainly the morning and afternoon, searching for food. In between they rest and perform other activities such as comfort behaviour. Dustbathing is a comfort behaviour which is usually performed in the middle of the day every second day (Vestergaard, 1982). The behaviour is carried out in a dry dusty substrate and through performing specific movements the dust gets in between the feathers and excessive feather lipids adhere to the dust which is then shaken off. This helps to make the plumage water resistant with a good insulating capacity (Liere & Siard, 1991) and it is also believed that dustbathing helps to remove ectoparasites. Before night falls the birds move up into a tree or other place high up to be protected from predators. Higher places can also be used as a resting place during day time. Fowl are seasonal breeders and the hen leaves the group to lay her eggs in a nest in a covered place where the eggs and later on chicks will be somewhat protected. After the chicks have hatched they follow their mother until 10-12 weeks old (McBride, Parer & Foenander, 1969).



Fig. 1. Domestic hens performing dustbathing (Photo Lena Wichman)

Motivation and animal welfare

Behaviour patterns that have evolved to increase the birds' survival are generally considered to lead to animals having a high motivation to perform them. Examples of such behaviour are to perch, lay eggs in a nest and dustbathe and researchers have investigated the laying hens need to perform these behaviours also in captivity. For example it has been found that hens housed indoors show a preference for using the highest perches, which is a sign that the anti predator behaviour still exists despite domestication (Newberry, Estevez & Keeling, 2001). In addition hens also work for the opportunity to roost on a perch during the night (Olsson & Keeling, 2002a) and show signs of frustration if access to perches is thwarted (Olsson & Keeling, 2000). Hens housed in cages which are provided with a nest decrease their pre-laying behaviour which is otherwise prolonged as the hen walks around and searches for a nest (Cooper & Appleby, 1995; Freire, Appleby & Hughes, 1996). Studies which have attempted to measure hens motivation to get access to litter for dustbathing have shown different results. Some imply that dustbathing has relatively low behavioural priority but overall most observations indicate that birds are motivated to perform dustbathing (see Olsson & Keeling, 2005 for a review). Performance of other behaviours apart

from the ones related to nesting, perching and litter are also of importance for birds' welfare, but they might not necessarily need a specific resource, except for sufficient space, to be performed e.g. preening and wing-flapping (Keeling, 2004).

All the behaviour patterns that an animal has evolved to perform in the wild do not necessarily need to be performed in captivity for the animal to have a good welfare. It has for example been suggested that prey animals in captivity most likely do not suffer from not having to escape from predators (Jensen & Toates, 1993). Although, it is important that they have the possibility to perform a behaviour if they are motivated to do so (Olsson, 2001). Different models have been proposed for how motivational drives are governed. The classic psychohydraulic model by Lorenz is mainly based on internal factors and that motivation builds up with time. This model has its limitations in explaining how functional feedback from the performance of carrying out a behaviour influences later motivation and other models were proposed which took into account the influence of external factors. For example Hughes & Duncan (1988) based a model on behaviour having an appetitive phase and a consummatory phase, where the consummatory phase leads to functional consequences which feed back to the motivation. Jensen & Toates (1993) argued that motivation is driven by both internal and external factors which can not be separated from each other. To get a broader picture of the behavioural needs of animals Jensen & Toates (1993) also point out that it is important to understand the feedback processes that shut off the motivation, and discuss these together with the goal representation the animal might have.

But how do we know what behaviours animals are motivated to perform? Observing the behaviour of animals can be a good indicator of what behaviours they are motivated to carry out. Laying hens can show signs of frustration in the form of gavel-calls (Zimmerman, Koene & van Hooff, 2000), stereotyped pacing and displacement preening (Duncan & Wood-Gush, 1972) if access to a wanted resource is thwarted. An example of this is that hens, which expected a food-reward but did not receive one, showed increased levels of locomotor behaviour and performed more gavel-calls than hens that received the expected reward (Zimmerman & Koene, 1998). It has been suggested that by performing pacing the animal is trying to repeatedly perform the behaviour and also to escape from the situation (Duncan & Wood-Gush, 1972). Another method to measure what an animal wants is by preference studies which present the animals possibility to choose between different options and so give an indication of whether, for example, they prefer one type of floor rather than another or whether a social companion is more important than the possibility to roost. This method however has its limitations as it might be that neither of the different options are valuable, but are chosen because of the lack of a better alternative. Consumer-demand theory has been suggested to be a good way to "ask" animals about their "behavioural needs" (Dawkins, 1983). Through different operant techniques as lever pressing, pecking a key or going through a weighted push-door, animals can show how high price they are willing to pay to perform a certain behaviour or get access to a specific resource. This would then show if the animal considers the resource to be a necessity or a luxury which would indicate whether or not they

would suffer if they can not get access to the resource or perform the specific behaviour (Dawkins, 1983).

When choosing a test method it is important that it is within the animal's cognitive capacity to couple the behaviour it is supposed to carry out with the reward (Fraser & Matthews, 1997). For example, pigs can be taught to press a nose plate to receive a food reward since rooting is part of their food search behaviour and hens which search for food by scratching and pecking in loose material on the ground can be taught to peck a key to get a reward. However, it might be difficult for a rat to connect that food of a certain colour will be poisonous whereas they could do the connection if the flavour of the food is different (Fraser & Matthews, 1997). One operant method which has been used and proved to work well in several studies where motivation of hens has been measured, is the push-door (Petherick & Rutter, 1990; Widowski & Duncan, 2000; Olsson & Keeling, 2002a; Jong et al., 2005). This method usually consists of a swing-door and the difficulty to open the door can be adjusted e.g. by weights. Generally the hen has to pass the door to get access to something on the other side. By testing the hen repeatedly with different weights a measure is achieved of how much she is willing to work to get access to the reward. It has been suggested that this method is suitable for hens as it resembles the natural situation where the bird can see what is on the other side (the resource they are working for) but might have to push through undergrowth in dense vegetation to reach it (Olsson, Keeling & McAdie, 2002).

Factors affecting bird welfare in commercial systems

Housing laying hens in modified cages and especially loose-housing systems is a step towards increased bird welfare as they provide the birds with the possibility to perform a greater variety of behaviour, but they are not problem free (Appleby & Hughes, 1991). Despite access to litter there can still be problems with feather pecking and cannibalism and in flocks of several thousands of birds this can cause serious damage to a large number of victims (Rodenburg et al., 2005). It is essential that the birds move around and find food and water which can be difficult when these are provided above ground (Appleby & Hughes, 1991). It is not uncommon that farmers close in the new pullets on the tiers where the food and water is placed for the first weeks to make sure that they find it (personal communication). This is a problem as it prevents the birds getting access to the litter area and also leads to a higher density than allowed by legislation.

There are several different factors that affect how well birds adapt in different housings. The design of the housing and management has a large impact (Zimmerman et al., 2006; Rodenburg & Koene, 2007) as does the genotype, with different hybrids behaving differently (Wall, 2003). Also the prenatal environment can have long term effects. For example the progeny of stressed hens showed greater fear levels and less ability to compete for food than chicks from non stressed hens (Janczak et al., 2006). Last, but not least, it has been shown that the first weeks of a chicks life, when many behaviours develop, are important for the later behaviour of the birds and many welfare problems originate from the rearing

environment of the chicks during these first weeks (Blokhuis & Wiepkema, 1998). According to Swedish Animal Welfare legislation chicks should be reared in a way which prepares them for the system they will be housed in as adults (DFS 2007:5). Exactly what this means is not evident. Birds might not necessarily need to be reared in the exact same housing as they will be housed in as adults. It may be more important that they are reared in such a way that prepares them and give them the ability to later adapt to and handle different environments and situations.

Ontogeny

Ontogeny can be described as the development of an individual from the moment the egg is fertilized and up to adulthood (McFarland, 1993). Even if behavioural development occurs throughout life, the first period in an organism's life is usually when most of the development takes place. The concept of critical periods, a short time span where certain behaviours could be developed, was initially proposed by Lorenz (1937), but after research in this area it is now regarded that the timing of development is more flexible than initially believed (Bateson & Hinde, 1999). However, even if the concept of developing a certain behaviour during a certain time is not applicable to all behaviours, it does have validity for many behaviour patterns. Some behaviours which are sensitive for being acquired during certain developmental periods and for which there has been a lot of research include social attachment (ducks, Lorenz, 1937; dogs, Scott, 1962), song learning in birds (Kroodsma, 1977) and language acquisition in humans (Lenneberg, 1969).

Today it is widely acknowledged that the development of behaviour is dependent on the interaction between genes, external factors and other internal factors. Evidence that the environment influence behavioural development is manifold and, for example by studying the development of the brain, it has been recognized that stimulation influences neural growth (Lewis, 2004). A case where this has created attention is in child development where it has been shown that babies who spend most of their first year in a crib developed abnormally slowly (Shatz, 1999). It is believed that the advantage of having neural activity dependent on environmental stimuli is that the nervous system can then be modified by experience and so has some degree of adaptability to the environment in which the organism develops (Shatz, 1999). There are numerous studies showing that early negative experiences, such as rearing animals in a poor environment, can have long term effects. Monkeys reared in social isolation show behavioural, cognitive, neurobiological and neuroanatomical deficiencies (see Gilmer & McKinney, 2003 for review). Rat pups exposed to social isolation show deficits in their later maternal and social abilities (Melo et al., 2006) as well as delays in the development of e.g. the dopaminergic system (Ellenbroek, Derks & Park, 2005). Barren environments with restricted possibilities for exploratory and food searching behaviour can lead to misdirected behaviours like tail biting in pigs (Weerd et al., 2006) and feather pecking in hens (Huber-Eicher & Sebö, 2001). Comparing animals reared in barren and enriched environments shows that the enrichment improves learning ability (pigs, Sneddon, 2000; mice, Iso, Simoda & Matsuyama, 2007) and neuroanatomy (e.g. brain weight, cortical thickness; see Rosenzweig & Bennet, 1996). Although, as development still occur all through

life some negative effects during rearing can be modified by events occurring later in life. For example middle aged mice have been shown to benefit from environmental enrichment with reduced age-related impairments in spatial memory (Frick et al., 2003).

Development of perching

In studies of feral fowl living under natural conditions it was observed that hens brooded their chicks in a nest on the ground during the first weeks. When the chicks had reached around six weeks of age the hen took them into the trees to brood them at night. This night time perching was preceded by the hen resting with her chicks on lower branches during day time from that they were one month old (McBride, Parer & Foenander, 1969). Experimental studies have compared perching activity between chicks together with a mother hen and chicks reared only together with other chicks. These have shown that when the mother hen perches the chicks follow her. This led to chicks with a mother hen beginning to perch earlier than the chicks without a hen since the hen used the perches (Riber et al., 2007), whereas the opposite result was found in another study where the mother hen did not use the perches so early and therefore the chicks in the only chick groups were quicker to begin to perch (Nørgaard-Nielsen, 1997a). Thus a mother hen influences chicks perching behaviour but might not always make them perch earlier than chicks reared without a hen. The ease of reaching the perches for the young chicks will also of course have an influence as they do not have a plumage adapted for flying. They can however jump between perches and in that way reach impressive heights even when very young (Wood-Gush & Duncan, 1976). Other factors which can influence perching are strain (Faure & Jones, 1982), and individual differences in perch use vary within strains, which suggests a genetic variance in perching behaviour. The design of the perch can also influence perching activity (Faure & Jones, 1982), as well as social dominance (Cordiner & Savory, 2001).

It has been suggested that there is a relationship between spatial ability and perching behaviour (Gunnarsson et al., 2000) and also that there is a sensitive phase when chicks learn to perch as the perch use of adults has been shown to be affected by their access to perches when young (Appleby & Duncan, 1989). Spatial memory and the corresponding neural system appear to be particularly prone to environmental influence (Gould et al., 2000). For example, it has been found in children that during school term there is a larger growth in spatial skills than during the summer (Huttenlocher, Levine & Vevea, 1998) and also how well children perform in a mental rotation test can be correlated to computer game experience (Quaiser-Pohl, Geiser & Lehmann, 2006). Manipulations of hoarding behaviour in two different species of hoarding birds has suggested that experience of food-hoarding is necessary for the normal development of the hippocampus which is a part of the brain that processes spatial information (Clayton, 1998). Scientific evidence for a link between environmental influence during a sensitive period on the development of the brain and spatial ability has been shown in domestic chicks reared either with or without opaque barriers when 8-12 days old. Chicks with opaque barriers showed an improvement in their spatial memory

when tested in a visual displacement test and a detour test compared to control chicks which had been provided with transparent barriers (Freire, Cheng & Nicol, 2004). This was reflected in chicks provided with opaque barriers being better at finding an imprinted stimulus when they had seen it being hidden behind one of two screens. These chicks also made fewer orientation errors when finding their way to the imprinted stimulus in a detour arena. In addition, chicks reared with opaque barriers had longer dendrites, with more spines, than chicks reared without visual barriers (Freire & Cheng, 2004). In these studies the spatial ability was measured on a two-dimensional level. Other studies have shown that early access to perches enhance the spatial development of chicks and increases the birds ability to solve a three-dimensional task (Gunnarsson et al., 2000). This has practical implications as it has been found that access to perches before four weeks of age decreases the number of eggs laid on the floor and the prevalence of cannibalism (Gunnarsson, Keeling & Svedberg, 1999). Also in an experimental task birds which had been reared with perches were better at avoiding a cannibalistic attack by jumping up on a perch (Yngvesson, Nedergård & Keeling, 2002). This all implies that being reared with perches improves the flexible use of three-dimensional space even if birds can learn to perch as adults. However, it has also been observed that there can be large individual differences in the use of perches (Faure & Jones, 1982; Yngvesson, Nedergård & Keeling, 2002). This could be due to individual differences in the tendency to learn this behaviour (Appleby & Duncan, 1989).

Development of dustbathing

Dustbathing consists of several specific movements. These different movements develop separately in the young chick during the first weeks and then become a functional unit (Kruijt, 1964). During week two and three chicks usually dustbathe several times per day (Hogan, Honrado & Vestergaard, 1991). After this dustbathing frequency decreases until around two months of age by which time the behaviour has stabilized at adult levels (Vestergaard & Hogan, 1992). Under semi natural conditions adult birds dustbathe every second day for around 30 minutes (Vestergaard, 1982) and the dustbath is preferably carried out in a dry substrate containing particles which can get into the feathers. Before a hen starts dustbathing the first tendencies preceding a bout are that she scratches and bill rakes in the dust. Subsequently the bird squats down and performs vertical wing shakes, leg scratches and head rubs. These movements are performed with fluffed feathers and aim to get the dust into the feathers and are generally called tossing behaviours. After repeating these sequences several times the behaviour is gradually changed into the next phase which is called the rubbing phase and mainly consists of side lying and side rubs. The side rubs are the movements which gets the dust rubbed against the feathers. Each phase is not always clearly separated and dustbathing movements as e.g. leg scratches and side rubs can be performed intermittently. A bout is usually finished by the hen standing up and performing a body shake which removes the dust from the plumage (Liere, 1991).

The exact form of a dustbathing bout varies between and within individuals and it can also be carried out differently depending on the substrate in which it is

performed (Liere, 1992). Hens housed without litter in e.g. conventional cages show sham dustbathing which is when birds go through the typical dustbathing movements in the absence of litter. This is found already in chicks which develop a dustbathing pattern irrespective of whether they are reared with access to litter or not. It can be questioned however if the behaviour is developed in the same way in chicks which develop sham dustbathing and chicks which learn to dustbathe in a functional substrate. Studies which have compared the dustbathing behaviour between birds reared with litter and without litter have given different results. In general the behaviour is performed in a similar way but differences such as the length of the bouts (Vestergaard, Hogan & Kruijt, 1990; Merrill & Nicol, 2005), number of bouts performed (Nørgaard-Nielsen, 1997b) and amount of side rubs performed (Larsen, Vestergaard & Hogan, 2000) have been found. In addition, comparisons of dustbathing behaviour performed on different types of substrates have shown that the quality of the litter has an effect on the dustbathing behaviour. For example Liere, Kooijman & Wiepkema (1990) reported that birds dustbathing in wood-shavings perform fewer side rubs than birds dustbathing in sand. This difference was interpreted as birds dustbathing on the less functional substrate (wood-shavings) having problems to come into the rubbing phase and so instead they kept restarting their dustbathing bout. This is probably due to that wood-shavings are too large to enter among the feathers and reach the skin of the bird, so performing rubbing in this case would not have had a functional effect.

Chicks do to some extent imprint on the substrate they learn to dustbathe on but, if given time and possibility, they can usually change their preference and choose the most functional substrate available to dustbathe in (Vestergaard & Hogan, 1992; Sanotra et al., 1995). Most birds reared with access to a good dustbathing substrate will use this for their dustbathing, but it has been observed that hens in modified cages perform their dustbathing on the wire floor instead of in the dustbath provided (Lindberg & Nicol, 1997; Olsson & Keeling, 2002b; Wall, 2003). Usually these birds have been reared in cages without litter so this finding may indicate that chicks might need to be reared with litter and learn to dustbathe in a functional substrate to fully use this resource. Another question is if a bird which has been reared without litter is content to perform sham dustbathing and considers this to be normal dustbathing. Some argue that sham dustbathing is a sign that birds have a behavioural need to perform dustbathing since it is performed even without practical feedback and that it is just an unsatisfactory attempt to perform an important behaviour (Weeks & Nicol, 2006). On the other hand it can not be ruled out that the performance of sham behaviours can motivationally satisfy the animal and be a replacement for the real behaviour (Hughes & Duncan, 1988), although later research has shown that this is unlikely the case, at least for birds reared on litter (Olsson, Keeling & Duncan, 2002). Nevertheless, it might be that animals which have never experienced a functional behaviour (i.e. were not reared on litter) do not know what they miss and to them sham behaviour is the normal behaviour (Weeks & Nicol, 2006). It has even been suggested that birds dustbathe in litter when given the opportunity because it is pleasurable, but that they might not necessarily have a need to dustbathe in litter (Widowski & Duncan, 2000).

Aims of thesis

The main aim of this thesis was to study the development of perching and dustbathing behaviour in laying hens. In commercial systems it is important that birds learn to use perches and can move around in the three-dimensional space to utilize the resources provided. The possibility to perform a normal dustbathing behaviour is also important for birds and the ability to use the litter can be affected by how the birds develop their dustbathing behaviour as young. Hence, how well laying hens learn to perform these behaviours might have long term consequences for their welfare as adult birds. In addition we also wanted to investigate these behaviours as they are interesting in their own right as examples of how different behaviour patterns develops at an individual level and in relation to specific resources.

There are two main parts in this thesis. The first one deals with the development of perching behaviour and is described in papers I and II. The second part deals with the development of dustbathing behaviour and is described in papers III and IV. The particular aims were:

- To study the individual development of perching behaviour to investigate what behaviours performed by a young chick influenced when it began to use perches. In addition we also investigated if different types of enrichment had an effect on when the chicks started to perch.
- To investigate the relationship between perching and spatial ability and more specifically if a chick starts to perch early because it hatched with a good spatial ability or if the spatial ability mostly develops through the use of perches.
- To study how access to litter, respectively lack of access to litter, at different periods during rearing influenced how birds developed their dustbathing behaviour.
- To investigate if birds which developed their dustbathing behaviour without litter would be satisfied to perform sham dustbathing or if they would be motivated to get access to litter if given the opportunity.

Material and methods

Animals

The laying hen hybrid Lohmann Selected Leghorn (LSL) was used in all studies. Birds were obtained from a commercial hatchery as newly hatched chicks and housed in the research facilities at Götala, Skara.

Housing, observations and test methods

Papers I and II

The same birds were used for Papers I and II. Ninety day-old chicks were allocated randomly to 18 pens (5 chicks / pen). The pens were 1.4 x 2.0 m large and contained two perches at 20 and 40 cm height, food, water, litter and a heating lamp. Six of the pens were CONTROLS and had no extra enrichment. FLOOR enrichment in the form of wooden blocks that the chicks could step up on were placed in six pens (Fig. 2) and the remaining six pens had HANGING enrichment as computer discs and plastic bottles hanging at beak height which the chicks could look and peck at (Fig. 3). These two different types of enrichment were chosen as the wooden blocks would be a way for chicks to physically practice going up on something and the hanging objects would attract the chicks attention to what was above their heads. Direct observations were carried out 12 times per day starting from 8 o'clock in the morning, one hour before lights were on, and then at regular intervals until seven in the evening, two hours after lights had gone out. Chicks were observed most days from day 5 until day 40. Each chick was individually marked and scan samples of where in the pen and what behaviour the chick performed was noted at each observation.



Fig. 2. FLOOR enrichment with wooden blocks on the floor
(Photo Anette Wichman)



Fig. 3. HANGING enrichment with CDs and plastic bottles
(Photo Anette Wichman)

To investigate the relationship between spatial ability and perching (paper II) two spatial tests were carried out. Firstly, a detour test when the chicks were three days old and had not yet begun to use perches and secondly, a radial maze test when they were 16 weeks old and all birds were perching. Each chick was tested once in each test. In the detour test the task for the chick was to find the way to its companions. The companions were in sight but the test chick had to turn away from them and walk around a barrier to reach them (Fig. 4). The time was taken of how long it took for the chick to solve the test but if they had not solved it within ten minutes the test was interrupted.

The radial maze consisted of eight similar arms spaced around a central arena (Fig. 5). In the outer end of each arm there was a bowl which contained a mealworm. After the pullet was released in the centre it had 20 minutes to walk

out into the end of each arm and eat the mealworm placed there. Notes were taken on how many visits into the different arms the bird needed to find all eight worms. Prior to the detour test no special training had been given and the chicks were naïve to the arena, but since the radial maze was more complex and the birds could be inhibited in their performance by being in a novel environment they were habituated to the arena. All the birds from one home pen were released together in the arena for half an hour on two occasions. During this habituation the bowls contained sun flower seeds so that the pullets should also learn that the bowls contained something tasty. In addition the pullets were also offered mealworms in the home pen and it was noted that all birds had eaten a meal worm before they were tested.



Fig. 4. Detour test with the test chick in the middle of the arena
(Photo Anette Wichman)



Fig. 5. Radial maze
(Photo Anette Wichman)

At eight weeks of age a tonic immobility (TI) test and at 14 weeks of age a runway test were carried out in order to compare the fearfulness and sociality of the birds with their performance in the spatial tests. The TI test was carried out in the home pen by gently holding a bird on its back in a cradle. After 10 sec the bird was released and the time it stayed immobile was taken. If a bird stayed immobile for more than ten minutes the test was stopped. The runway test consisted of a 3.5 m long corridor where a single bird was released in one end and the other pullets from the same pen were placed behind a net in the other end so that they were visible for the tested hen. Each bird was tested for ten minutes and as a measure of their sociality it was noted how quick they were to approach the other hens and how much time they spent close to them. When birds were 18 weeks old they were moved to larger pens with perches provided in a more varied complex layout (Fig. 6). Perches were placed at 20, 40, 50, 90 and 130 cm height and could be reached directly from the floor or by jumping from one perch to another. This move to new pens was an attempt to copy the situation when pullets are moved from the rearing house to the laying house where they have to adapt to a new environment. For the first five days after birds had been moved to the pens it was observed at what height the birds perched and how they moved between perches during day time. Additional observations of night time perching were carried out from night one to ten.



Fig. 6. Large pen with perches at different heights
(Photo Anette Wichman)

Papers III and IV

For Papers III and IV 48 chicks were housed in groups of four in 12 pens similar to those used for the control treatments in paper I, although this time there was no litter on the floor. Instead each pen contained a wooden box which contained either peat (6 pens) or a sheet of corrugated paper (6 pens). Peat is a preferred substrate for dustbathing and is referred to as the Litter (L) treatment and the other pens with boxes with paper are referred to as the Non litter (N) treatment. A wire netting floor was placed five cm over the concrete floor of the pens when the chicks were two weeks old to prevent them from dustbathing in dust or food spilled on the floor. Birds were filmed at around six weeks of age for six consecutive days and dustbathing behaviour was observed from the videos. Before the filming began new treatments were created by regrouping the birds so half of the birds from peat were moved to pens with corrugated paper and half of the chicks previously kept on corrugated paper were moved to pens with peat. Thus we had four treatments based on the birds experience of peat (1) Having access to peat all their life (LL), (2) Never having experienced peat (NN), (3) Being reared on peat until around six weeks of age (LN) and (4) Gaining access to peat around six weeks of age (NL). Birds remained in groups of four with two birds from one treatment sharing pen with two birds from another treatment so that LL and NL birds were housed together (Fig. 7) and NN and LN chicks were housed together (Fig. 8).



Fig 7. Litter treatment with LL and NL birds
(Photo Anette Wichman)



Fig. 8. Non litter treatment with NN and LN birds
(Photo Anette Wichman)

After filming the birds were kept in the same groups as they had been filmed in and with the same material (peat or paper) in the wooden box. When birds were 16 weeks old the filming was repeated to investigate if and how the birds' dustbathing had changed after having been exposed to the same treatment for a longer time. From the video recordings it was observed how often and for how long the birds carried out a dustbathing bout. The first dustbathing bout performed for each observation period was selected for detailed observations on the different components such as side rubbing, lying still and vertical wingshakes and leg scratches. The vertical wingshakes and leg scratches were combined and are referred to as tossings. It was also observed if the bird finished the bout by performing a body shake.

To test whether the birds' motivation to get access to peat to dustbathe in depended on previous experience of litter, a follow up experiment was carried out on the same birds as in paper III when they were 27 weeks old. The method chosen to test the birds' motivation was the push-door. The push-door was placed in a test arena between a start area and a goal area (Fig. 9). To reach the goal area the birds had to pass through the push-door and during testing the reward in the goal area was a wooden box containing peat. Before testing started, the birds were trained to go through the push-door and accustomed to the test arena. To make them motivated to pass the door they were food deprived for some hours and the reward in the goal area was food. After several training sessions all birds had reached the criteria to go through the door three times in quick succession. During training there was no resistance on the door. Five days prior to the start of the testing all birds were deprived of peat so their only possibility to perform a functional dustbath in litter was when tested. Each bird was then tested in the push-door once every fifth day in a series with increasing resistance of the door of one Newton for each trial. A bird was tested until it failed to go through the door and then the highest level of resistance it had actually pushed through was used as the measure of how motivated the birds was to dustbathe in peat. In addition notes were taken on latency time to go through the door and if it dustbathed or not and latency time to begin dustbathing. They had 20 minutes to pass the push-door after having been released in the start area and 40 minutes to begin dustbathing after having passed the push-door. When a bird had begun a dustbathing bout the test was not stopped before the bird had finished the bout and stood up again. There were four push-door arenas so that four birds were tested at the same time in the same room, but one in each arena.



Fig. 9. Hen going through the push-door
(Photo Anette Wichman)

Statistical analyses

The statistical analyses are described in more detail for each paper, but a short description is presented of the main method used in each of the different papers.

In Paper I Analysis of Variance was used to analyse the effect of treatment on start of perching as well as the behavioural data. For the treatment analysis group mean was used as the statistical unit. Only data from the first three weeks were included in the analyses of how the individual behaviour related to start of perch use since by the end of week three most of the chicks had already begun to perch. For these analyses of individual behaviour each chick was a statistical unit with treatment used as a fixed effect and pen as random effect.

As we wanted to investigate the relationship between many different variables on an individual level data in Paper II were analysed with Principal Component Analysis. Two PCAs were carried out. Both were based on Spearman correlations as data were not normally distributed. The first PCA contained 11 variables which had the same number of observations i.e. all birds have data for all variables. The second PCA was carried out on 12 variables of which some had different numbers of observations. The variables included in the two PCAs are mainly the same, except for the variables from the radial maze. As some birds did not enter all eight arms in the radial maze they had missing data for some variables e.g. the number of entrances to different arms needed to find all mealworms. Therefore this second PCA was carried out where also the variables of the performance of the birds in the radial maze where birds had missing data could be included.

Data in Paper III were not normally distributed so the variables latency to first dustbath, number of bouts, side rubs, tossing and lying still were analysed using a Poisson distribution. Duration was analysed using a gamma distribution and body shake was analysed using a binomial distribution. Analyses were carried out using estimated generalized linear regression models. For most of the analysed variables both observation periods were included by modelling the dependency of the second observation period on the first observation period by incorporating the pairing of observations at both observation periods for each individual. The LL treatment was used as an intercept for most of the analyses and therefore the comparisons are between the LL and the other treatments.

In Paper IV data was normally distributed so differences between treatments in the maximum resistance that hens pushed open was compared using a GLM with early and late experience of peat as fixed factors and the interaction between these factors.

Summary of results

Paper I

All chicks but one were seen perching during the observations from day 5-40 (Paper I). The mean day for all birds to start perching was 15.6 days and the first chick was seen on a perch at day 8. It appeared as chicks which had FLOOR enrichment started to perch earlier (13.8 days) than CONTROL chicks (17.3 days) and chicks which had HANGING enrichment (16.6 days). However this difference was not significant ($p = 0.21$). From the behavioural observations it was shown that some of the chicks' behaviours were related to when they began to perch. There was a positive association between time spent under the perches the first two weeks and an early start of perching (week one $t = 2.7$, $p = 0.014$; week two $t = 2.4$, $p = 0.025$). Also the number of observations the chicks were seen on the perches weeks two and three related positively with an early start of perching (week two, $t = 5.6$, $p < 0.001$; week three, $t = 4.3$, $p < 0.001$). On the other hand, chicks which had more social interactions with the other chicks week three were later to begin perching ($t = -3.2$, $p = 0.002$) and also chicks that spent more time under the heating lamp during day-time the first three weeks were later to begin perching (week one, $t = -2.7$, $p = 0.01$; week two, $t = -3.4$, $p = 0.001$; week three, $t = -3.6$, $p = 0.001$).

Paper II

Forty out of the 90 chicks solved the detour task in a mean time of 236 seconds and in the radial maze 31 out of 87 hens managed to find all eight mealworms. When moved to the new larger pens on average the birds spent 27.1% of their time on a perch during day time and the most used heights were 50 and 90 cm. During night time there was an increasing trend for use of perches and from night seven to ten all birds roosted on a perch and there was also a trend to use the highest perches. From the multivariate analyses which investigated relationships between the birds early and late perching behaviour with performance in the spatial, (detour and radial maze), fear (TI) and sociality (runway) tests (Paper II), the most important finding was that the perching behaviour of older birds was related to their performance in a two-dimensional task. This was suggested by loadings from a variable from the late perching observations (how much the birds perched as adults during the first two hours when they had been released in the new pens) and radial maze test (how many correct choices out of the first eight choices a bird made) being loaded quite strongly in the same direction. There was also a relationship between the TI test and how many arms the birds visited in the radial maze with more fearful birds entering fewer arms than less fearful birds. There were no indications of a relationship between early perching, late perching and performance of the chicks in the detour test or the runway test.

Paper III

From the study of development of dustbathing behaviour and how it was affected by access to litter (Paper III) it was found that chicks which had lost access to litter

(LN) performed their first dustbath during the observation period around one day later than the chicks in the NL treatment ($z = 3.09$, $p = 0.002$). Most of the dustbaths were performed in the wooden box. During the first observation period some dustbaths were performed on the wire floor by chicks from the NN, LN and NL treatment but the LL birds performed all their bouts in the wooden box. In the second observation period all dustbaths were performed in the wooden box, irrespective of whether this contained peat or paper. There was a significant difference in the mean length of the bout between the first and second observation periods with an increase in time from 19 minutes in the first observation period to 30 minutes the second observation. The mean duration of the bout did not differ between treatments neither for the first or second observation period. But for the LN birds (lost access to peat) there was a significant interaction for the first and second observation period in the mean duration of a dustbathing bout. They changed from having the longest mean duration the first observation period to having the shortest the second observation period ($W = 4.1$, $p = 0.042$). Interestingly, there was a significant difference between treatments in the variability of the duration of a dustbathing bout for both observation periods. Birds from LL and NL (currently kept on peat) were similar and had a small variation in the duration of a bout whereas NN and LN birds (currently kept on paper) behaved similarly and performed more extremely short or long bouts ($W = 17.9$, $p < 0.001$). In addition, the detailed observations of the dustbathing bouts revealed that a dustbath performed in peat contained a higher proportion of side rubs than if carried out on paper. This was not tested separately for each observation period (due to many outliers) but the pattern was similar both in the first and second observation period ($z = -5.7$, $p < 0.001$). There was no significant difference between treatments in the proportion of tossings performed in a bout, but there were some differences in how much birds lay still during a bout. The first observation period the LL birds performed less lying still than the other treatments and the second observation period the LN birds performed more lying still than the other three treatments. Regarding the observation of how the birds finished their dustbathing bout there was a tendency that LN birds less often finished their bouts by performing a body shake than LL birds. There were also a numerical pattern indicating overall difference with LL and NL being similar and more often finishing their dustbathing bout with a body shake than NN and LN birds which were similar to each other.

Paper IV

During training all birds successfully learned to pass the push-door (Paper IV). When testing began most of the birds which had no or only early experience of peat needed one or more trials to begin to dustbathe in the test whereas birds with recent experience of peat dustbathed from the first trial. A few birds from the NN and LN treatments finished the test after a small number of trials without having dustbathed (except for one hen that dustbathed once and then stopped going through the door). Despite this there was no difference in the mean resistance birds from the different treatments pushed open to reach the dustbath. Thus there was no difference between these birds with different previous experience of litter, neither depending on whether they had access during early rearing ($F_{1, 24} = 1.08$, p

= 0.31), late rearing ($F_{1,24} = 0.34, p = 0.57$) or the interaction between these ($F_{1,24} = 0.01, p = 0.91$). The mean resistance the birds pushed open to get access to the litter was 13.9 Newtons and after having passed the door on most occasions the bird had a short latency before starting a dustbathing bout.

General discussion

In this thesis the ontogeny of perching and dustbathing behaviour has been investigated. The findings concerning perching behaviour point to some different factors that relates to the initiation of perching and how spatial ability is related to use of perches in laying hens. In addition, indications of how access to litter influences birds dustbathing behaviour and how this could affect their welfare have been found. In this general discussion, firstly, the results found in the two papers dealing with how development of perching is related to different factors are discussed in relation to previous knowledge about this subject. Then the results from the two papers dealing with the development of dustbathing are discussed in the light of the influence of peat on development and on bird's later motivation to dustbathe in peat. Following on from this some comparisons of how external resources influence perching and dustbathing behaviour are made. Finally, methodological considerations are discussed.

Development of perching behaviour

Behaviours related to start of perching

As it has been observed that there is individual variation in how much birds use perches (Faure & Jones, 1982) we were interested in investigating perching behaviour on an individual level. From the observations of how chicks behaved in the home pen the first weeks it was found that some behaviours related to when they were first seen on a perch. Chicks that spent more time under the perches and less time under the heating lamps the first weeks were quicker to begin perching. Also chicks with fewer interactions with other chicks were quicker to begin perching. These chicks with less social interactions might have started perching earlier because they wanted to avoid other chicks and did this by jumping up on the perches. It is known that perches are used as a way to escape from cannibalistic attacks (Yngvesson, Nedergård & Keeling, 2002) and low ranked birds use perches to avoid more dominant birds (Cordiner & Savory, 2001). Or they possibly had fewer interactions with other chicks as they spent more time on the perches. The finding that chicks spending more time under the perches and less time under the heating lamp used the perches more, could be interpreted as birds which were more exploratory and going under the perches more often would ultimately explore the perches by jumping up on them. But this could also be interpreted the other way around that birds which perched more also spent more time under the perches because they were frequently moving to or from the perches. However, the finding in paper II, that birds which used the perches more when moved into the new pens as pullets were those individuals better at finding

the mealworms in the radial maze, suggests a link to exploratory behaviour and supports the first explanation, that a high degree of exploratory behaviour enhances the utilization of perches, rather than the second interpretation.

Day time and night time perching

In our study half of the observations were carried out when lights were on but since each pen contained a heating lamp which gave off some light the birds could still see, move around and be seen during the so called night time observations. Despite this, it is interesting that all chicks were seen for the first time on a perch during a day time observation. This resembles the natural situation where the mother hen takes the chicks to rest on lower branches during day time before they start the night time roosting. As our observations ended when birds were around six weeks old, the age when it is normal for chicks to begin night roosting, it is not surprising that most of the chicks were on the floor under the heating lamp during night time observations. This is probably also connected to the need for warmth by young chicks. If they have a mother hen they can still sit underneath her and get some warmth even when they are up in a tree whereas our chicks only got extra heat under the lamps on the floor.

Effects of enrichment on perching

Appleby & Duncan (1989) argued that using a perch for the first time is something that has to be learnt and is separate from physical skill since birds which start to perch can do so without difficulty. They suggested that it is the mental part of using a three-dimensional space that chicks have to learn if they have only moved on one level previously. However, mental ability is probably connected to physical activity even if it is not connected to physical skill per se. For example Bjorklund & Brown (1998) discuss a possible link between physical activity and development of cognitive abilities in humans and hypothesize that gender differences in spatial ability are dependent on the different types of physical play usually engaged in by boys and girls. Likewise it has been found that chicks need to interact with barriers i.e. move around themselves and get out-of-sight behind the barriers, for there to be an effect on the chicks' spatial ability. Just observing objects disappearing behind a barrier did not enhance development (Freire, Cheng & Nicol, 2004). The environmental enrichment provided in our study did not have a significant effect on the start of perching but there was a numerical difference where chicks which had access to wooden blocks were quicker to begin perching than chicks in the control and hanging enrichment treatments. This could leave room for speculation since this was the most physical of the treatments. It would have been interesting to use the same treatments but perches that were more difficult to reach to investigate if more clear differences between treatments had appeared. The perches used in the rearing pens were rather low and so easy to discover and jump up on for the chicks. This might have led to there not being enough variation between the chicks perching behaviour to pick up possible benefits of the treatments.

Spatial ability and perching

Previously a relationship has been found between early access to perches and a later flexible use of the three-dimensional space (Gunnarsson et al., 2000). A relationship has also been demonstrated between two-dimensional enrichment, in the form of barriers, and two-dimensional ability measured in some spatial tests (Freire, Cheng & Nicol, 2004). From the findings in paper II we can now add that there seems to be a relationship between two-dimensional spatial ability and perching, which is a three-dimensional skill. This was shown as the birds which used the perches the most two hours after having been released in the new bigger pens also needed fewer visits to different arms in the radial maze to find all eight mealworms. This finding seems logical as one would expect there to be an overall connection between different spatial abilities. However to our knowledge this type of comparison between physically carrying out a three-dimensional and two-dimensional task has not been done before. In humans comparisons of different types of spatial abilities tested using pen and paper found moderately high correlations between spatial visualization, spatial relations and perceptual speed (Miyake et al., 2001). The spatial visualization task required a complex sequence of mental manipulations, for example depicting what an unfolded paper (two-dimensional) would look like if folded (three-dimensional). The spatial relations task included spatial transformation of two-dimensional figures and the perceptual speed task aimed to assess how fast a person could make a relatively simple judgement of different patterns which did not need to be mentally rotated. These three spatial tasks thus measure slightly different spatial abilities including both some type of three-dimensional and two-dimensional task. This could support a link between two-dimensional and three-dimensional ability also when the tasks involve some physical effort (i.e. walking or jumping).

Interestingly we only found a relationship between the birds' use of the perches and their performance in the spatial tests when the birds had just been released in the new, larger and more complex pens. The lack of relationship between spatial ability and use of perches when the birds were familiar with their housing indicates that it has to be a challenging situation for differences in spatial ability to have any evident influence on the birds' behaviour. It is also in accordance with the findings in a study of humans performing a spatial task where differences in spatial skills were only apparent when the task was complex (Wanzel et al., 2003). It was also evident in the study by Gunnarsson et al. (2000). In that study the hens had been reared with or without perches and then all birds got access to perches at eight weeks of age. Initially birds reared without perches had some problems to learn to perch, but after a time they were using perches in their home pens similarly to the birds which had been reared with perches. Despite this, the birds reared with perches outperformed the other birds when they were later tested in a new complex spatial task which involved moving between different levels in the three-dimensional space. This was interpreted as birds which had learnt to perch as young being more flexible in their later perching behaviour. An analogy could be made between language skills in humans. Adults have the capability to learn new languages but most often this language will never be used with the same ease and nuance as the person's native language.

In the perching study we also aimed to investigate whether the individual variation in the birds use of perches was mostly due to innate spatial ability already at hatch or whether chicks spatial ability mostly develops through the use of perches. Unfortunately we did not find any relation between early spatial ability, as measured in the detour test, and early perching. Neither did we find any relationship between the birds early perching and their performance in the radial maze. Thus we can not say whether spatial ability is mostly innate or developed through the use of perches. It could be that these factors are too joined to be separated out and that our attempts to do this were in vain. Alternatively, it could be that the methods used failed to detect these different influences. As already mentioned, one possibility is that the early perching was so easy for the birds that this measure did not distinguish between different degrees of spatial ability in the young chicks and therefore no relationship between early perching and the birds spatial ability as measured in the detour test could be found.

In summary, several different aspects of bird behaviour were found to be in the perching related to the development of perching. There were indications that more exploratory behaviour, shown as time spent underneath the perches, was connected to an early start of perching. Chicks were also seen on a perch the first time during day time observations, which supports that the first use of the three-dimensional space takes place when birds are active and moving around more. In addition, in the adult birds there were indications of a relationship between how much they used perches when first put into a novel environment and how well they solved a two-dimensional task.

Development of dustbathing behaviour

Effects of access to peat during rearing on dustbathing behaviour

When comparisons were carried out of the dustbathing behaviour of birds which lost and gained access to peat it was found that birds changed their dustbathing behaviour. Already during the first observation period when the birds had just been exposed to the new treatment they behaved similarly to birds which had remained on the peat or on paper. For example the variation in the duration of a dustbathing bout was similar between birds that had never had litter (NN) and those that lost access to litter (LN) but differed to the birds which always had access to litter (LL) or gained access to it (NL), which on the other hand were similar to each other. The birds without litter had a larger variation in the duration of their bouts and carried out more short and long bouts than the birds dustbathing on peat. The birds dustbathing on peat performed more coherent dustbathing with most bouts being similar in their duration. The reason for the larger variability in the NN and LN treatments is probably due to lack of feedback from litter. Either birds interrupt their bout or they prolong it, as though restarting over and over. This fits with the result that the proportion side rubs performed in a bout was higher for birds dustbathing on litter. Side rubbing occurs later in the dustbathing sequence and it has been suggested previously that if birds dustbathe in litter consisting of particles which are too large to enter into the feathers, or when there

is no litter, the birds will not get adequate feedback and so never reach the phase where tossing behaviour goes over into rubbing behaviour (Liere, 1992). This feedback mechanism can be a way for birds to cope with different qualities of dust but it also implies that hens probably perceive whether they are getting a functional feedback from the behaviour or not.

Other studies have found that there can be long term effects of the rearing environment and that a bird's dustbathing pattern can be affected even after getting access to litter. In our study most of the dustbathing behaviour changed when birds changed substrate and in most cases the chicks adopted a similar behaviour to the chicks which had remained on the same substrate. However, some differences did occur which suggested that birds which had lost access to litter (LN) might have had some additional negative experience by having to perform sham dustbathing compared to birds which had never experienced litter (NN). For example the LN birds waited the longest before dustbathing when they had just lost access to peat and this treatment differed the most between the two observation periods in the mean length of their bouts. In addition LN birds also persisted in the second observation period in interrupting their dustbathing bouts by lying still whereas the NN birds were now similar to LL and NL birds in this behaviour. On the other hand, the NL birds which gained access to litter were the quickest to begin dustbathing when they just got access to litter and also did not differ from the LL treatment in any behaviour the second observation period. This suggests that if given easy access to a good functional substrate birds would probably utilize this and begin to carry out "normal dustbaths" whereas birds that lose access to something valuable might have more difficulty to adapt to the situation. However some concern can be raised about the ease with which our birds adapted to gaining access to litter as the age of the bird at the change of substrate might have some influence. Our birds were rather young when exposed to the new treatment and there were indications that their dustbathing behaviour was not fully stabilized. The mean length of a bout was shorter in the first observation period than in the second observation period when the mean length of a bout was similar to that observed in adult birds housed under semi natural conditions (Vestergaard, 1982). This could have made them more flexible in adjusting their dustbathing behaviour. However, Johnsen, Vestergaard & Nørgaard-Nielsen (1998) found that birds which had been reared on wire for only four weeks, i.e. were younger than our birds, showed long term effects on their dustbathing behaviour. This could indicate that other factors apart from age might influence how much birds change their dustbathing behaviour. For example, the contrast between wire and sand in the Johnsen, Vestergaard & Nørgaard-Nielsen (1998) study may have been larger than the contrast between the two treatments provided in our study. As it also has been shown that birds dustbathe differently on different types of litter this should be taken into consideration when comparing dustbathing and sham dustbathing (Petherick & Duncan, 1989). For example the description by Liere, Kooijman & Wiepkema (1990) of birds dustbathing in woodshavings is similar to the sham dustbathing performed by the birds in our study.

Do birds have a need to dustbathe in litter?

In the push-door experiment all birds from the LL and NL treatments (which had been deprived of peat for five days) dustbathed already in their first test trial. Birds from the other two treatments, the NN and LN birds were surprisingly similar in when they first began to dustbathe. One NN hen dustbathed the first trial and most of the other NN and LN birds dustbathed in the second trial. This implies that the chicks which had dustbathed on peat the first five weeks of their life had by now “forgotten” this and appeared to be as naïve to litter as the chicks which had never experienced peat before. This seems contradictory to the finding that the LN birds which had lost access to litter, showed signs in their dustbathing behaviour indicating that they had another perception (memory) of how a dustbath should feel like than the NN birds, which had never experienced peat. The finding that they did not respond differently than NN birds when they encountered peat again could indicate that they had by now, 10 weeks after the last sham dustbathing observations had been carried out and 20 weeks after their last experience of dustbathing in peat had “forgotten” this feeling. An alternative explanation could be that there are two different types of “memories” with the feeling of what a dustbath should be like on the one hand and the exact image of what a particular dustbathing substrate looks like on the other hand that brings about these differences.

There were individual differences in how much experience birds needed with the peat before they began to use the peat to dustbathe in. One NN bird and one LN bird went through several trials before their first dustbath and one NN and one LN bird never dustbathed in the test. But overall, most birds soon (after around an hour with access to the peat in the push-door test) started to perform functional dustbaths when given opportunity. Despite these differences in when they first dustbathed in the push-door test between the birds which had recently had access to peat (LL and NL) and birds which had no or only early experience of peat (NN and LN), there was no significant difference in the resistance birds from the different treatments pushed open to get access to the goal box with the peat. This shows that after dustbathing just once in a functional substrate birds were as motivated to continue to do this as birds which had always dustbathed in peat.

When the birds were tested for their motivation to dustbathe in peat they had free access to perform sham dustbathing in the wooden boxes in their home pens. But despite this, birds from all treatments pushed through high resistances to reach the litter. Birds pushed open approximately the same resistance in our study as did birds in another study that measured the motivation of birds which had been food deprived for 24 hours (Olsson, Keeling & McAdie, 2002). In addition, after having passed the door birds used the peat for dustbathing and began dustbathing shortly after having entered the goal area. This supports the findings of Matthews et al., (1993) and Jong, Fillerup & Reenen, (2005) that birds have an inelastic demand for peat, which means that dustbathing in a functional substrate is not a luxury for hens but a need. Hence, it appears that laying hens are willing to pay a high price to perform functional dustbathing and that this can not be replaced by sham dustbathing.

In summary, the results from the dustbathing studies show that even if birds are reared without peat most of them will when given the opportunity perform their dustbaths in this substrate. After having started to dustbathe in peat they will be as motivated to dustbathe in peat as birds that have been reared with peat. When birds perform sham dustbathing the duration of the bouts are more variable and in general a more irregular dustbathing pattern is seen. This all implies that birds differentiate between functional dustbaths and sham dustbathing and that sham dustbathing is not motivationally satisfactory even for birds which have been reared without litter.

Comparison of development of perching and dustbathing

Importance of access to resources

As perching and dustbathing behaviour are different in many aspects it is difficult to compare these behaviours with each other. Also, the studies in this thesis were designed to investigate these behaviours separately with emphasis on how perching develops on an individual level and its relation to spatial ability and how dustbathing develops depending on whether it can be performed in a functional context or not. However, several interesting aspects regarding comparisons between perching and dustbathing merit some thought. Most findings points to that the development of the different dustbathing movements is prefunctionally governed, i.e. it is innate and will develop despite functional feedback (Hogan, 1999). But the pattern of the proportions of the different movements is flexible and changed according to the substrate the dustbathing is being performed in. Perching on the other hand needs to be practised by the young bird to enhance the mental three-dimensional spatial skill and a later flexible perch use (Gunnarsson et al., 2000). Thus the development of perching but not dustbathing is dependent on external resources. However, if one looks at it in another way, chicks can hardly perform sham perching movements if they do not have anything to jump up on whereas they can perform the dustbathing movements without litter. An interesting speculation is what would happen with the development of dustbathing behaviour if chicks were prevented from performing any dustbathing movements as young. Would they still perform these movements in the same way as older even if they could not perform them the first three weeks when the behaviour usually develops? Another speculation is that it is not unusual under commercial conditions that perches are placed just above floor (or cage) level or provided as a bar within a tier. Might this be something equivalent to sham perching in that the bird has the posture of perching? It is questionable whether the bird receives the appropriate perching feedback and that such a perch would fulfil the bird's need to perch. If one compares with what has been found about sham dustbathing not being able to replace real dustbathing, the answer would probably be no.

Is it possible to miss something one has never experienced?

An important issue regarding animal welfare is whether an animal can have a perception of and miss something it has never had. For example, would a bird which has never perched miss perching? This is almost impossible to answer since

how does one test if an animal wants something without in some way showing it or giving them the possibility to reach it? However, by observing goal directed behaviour researchers have gathered some evidence that animals which have experience of something can have a representation of this when it is not in sight (for a review see Shettleworth, 2001). For example two different studies have suggested that laying hens might have a perception of litter even when they can not see it (Nicol & Guilford, 1991; Petherick, Waddington & Duncan, 1990). In our study one of the treatments consisted of birds reared without litter and only being given experience with litter in the test situation. This was to minimize their experience with litter and the results showed that even after very little experience of dustbathing in peat these birds were just as motivated to dustbathe in litter as birds which were reared and had always dustbathed in peat. These findings, that birds may have a perception of litter even if they do not see it, and the finding that when given opportunity litter inexperienced birds will work for litter as much as litter experienced birds leaves room for speculation. It does not seem unreasonable that even totally naïve birds might have some kind of sense of missing something (in this case litter) that during the course of evolution has been very important for survival, even if they do not necessarily have an exact image of what it is they are missing until they see it. Supporting the hypothesis that hens might miss something they have never experienced is the finding that whether or not laying hens had previous experience of a nest did not influence their pre-laying behaviour when deprived of a nest (Cooper & Appleby, 1995).

Methodological considerations

Spatial tests and perching observations

The spatial tests in paper II were chosen because they had been developed and used previously to measure spatial ability. Especially the detour test has been used in several studies on young chicks (e.g. Scholes & Wheaton, 1966; Regolin, Vallortigara & Zanforlin, 1994). The radial maze has mostly been used in rats (e.g. Olton, 1987) but also for other species like cows (Bailey et al., 1989), poultry (Zimmerman et al., 2003) and for comparison between different mammals and birds (Lipp et al., 2001). However, both the detour test and the radial maze have mainly been used to test spatial learning and memory. This requires repeated exposure to the test, although chicks have been tested for problem solving in the detour test and showed that they can do it in a single trial (Regolin, Vallortigara & Zanforlin, 1995). In our study we were interested in the ability of the birds to solve a spatial problem and therefore only wanted to test them once. This was also the reason for using two different types of tests, one before the chicks started to perch and one afterwards, instead of using the same test at the two different ages.

As with all tests it can always be questioned whether one actually measures what one intends to or if there might be other variables not taken into account that influence how the animals perform in a test. This was the reason why we also tested the birds in the Tonic Immobility (TI) and Runway tests. These tests measure fear (Jones, 1996) and sociality (Jones et al., 2002). There were no indications that the behaviour of the chicks in these tests had any relationship with

how the chicks performed in the detour test. This implies that the detour test measured the birds spatial ability. Furthermore, as approximately half of our chicks managed to solve the task the implication is that it had an appropriate level of difficulty which made it possible to identify differences between individuals. The radial maze was an even more challenging task as only a third of the pullets managed to find all the eight mealworms. However, here we did find a relation with the TI test. Birds with longer TI times (more fearful) also visited fewer arms in the maze. This shows that birds which found very few mealworms did not necessarily have a bad spatial ability but may have been inhibited by fear from entering out into the different arms. Therefore this was taken in consideration in the analyses and only birds which visited at least eight arms (even if these were not necessarily eight different arms) were included in the second Principal Component Analysis. As we found a relationship between the performance of these birds in the radial maze and their perching behaviour it indicates that the radial maze did measure their spatial ability.

There was no correlation in the performance of birds in the detour test and their performance in the radial maze. However, in hindsight we would probably still use the same two spatial tests as to my knowledge there are no better spatial test developed and validated. Although, since both the detour and radial maze have mainly been used to test spatial learning and not problem solving in one trial, it would be interesting with further validation of these tests and especially how they relate to one another, perhaps by performing the tests on birds of the same age. The result from this study proves them to be promising. The reason that there was no relationship between early perching and the two spatial tests could, as discussed previously, possibly be due to lack of variation in the measure of the chicks early perching, both in when they first started to perch and in how much they perched during the first weeks, rather than being due to a lack in the spatial tests themselves.

Treatments and observations of dustbathing behaviour

Many studies have compared the dustbathing behaviour of birds on different types of substrates with no access to litter, where wire has usually been used as the non litter treatment. In this study we used a box with a sheet of corrugated paper as the non litter treatment in an attempt to measure the difference between litter and non litter only depending on whether or not the birds got functional feedback from their dustbathing. By using the wooden box we tried to have the surface they performed the behaviour on as similar as possible for the different treatments. It can not be ruled out that the birds might have received some feedback from dirt in the box even if it was cleaned regularly but this was probably negligible in comparison to the feedback birds dustbathing on peat received. In addition, having the chicks accustomed to dustbathing in the wooden box probably was a benefit as the birds were not fearful of the way the peat was presented when they had their first experience of it. In a study by Petherick et al. (1995), chicks which were inexperienced with peat readily dustbathed when it was presented underneath the wire floor but when a box with peat was placed in their cage for one hour the birds did not utilize the peat as they seemed to be fearful of the box.

When birds were regrouped at around six weeks of age and the two new treatments, NL and LN, were created, birds from different treatments came to share pens. The LL and NL birds on the one hand were sharing pens and on the other hand NN and LN birds were housed together. The chicks in the same pen could be assumed to have some influence on each others dustbathing behaviour. This could be an argument for why LL and NL birds were similar in their dustbathing behaviour as well as NN and LN birds being similar in their dustbathing behaviour. However, if this had been the case we would not have expected the significant differences found between the groups but rather that all groups would have been rather similar independent of treatment as all pens contained birds with different previous experience of peat and paper. Thus the social influence of the chicks dustbathing behaviour was probably of minor consequence compared to if they had current access to peat or paper.

Push-door

We chose the push-door method to measure the birds motivation to get access to peat to dustbathe as it has been used before with good result. Also in our study the method worked well. All birds learnt to pass the push-door during training and performed in the test despite being in social isolation. During testing the birds could hear the other birds which were being tested at the same time although there were no indications that this would have affected their dustbathing behaviour. Apart from those trials before the NN and LN birds had begun to dustbathe, birds almost always began dustbathing shortly after having passed the push-door. Thus one can reasonably conclude that the reason why birds were motivated to pass through the door was to dustbathe in the peat. Further supporting that the test did indeed measure motivation to dustbathe was that it is the birds which did not dustbathe in the test which were the first ones to stop going through the door. Only one bird dustbathed once and then stopped going through the door. All the other birds which dustbathed in the test did not begin to fail to go through the door until the resistance was fairly high (around 14 N).

Conclusions

Results in this thesis point to more exploratory individuals being quicker to begin perching and individuals with good spatial ability using perches more when they come into a new environment. All birds used perches and it had to be a new challenging situation to find differences in individuals' spatial ability. This supports that if birds are reared with perches they will use them and this will have positive effects on their later use of perches. Birds performing dustbathing on peat show a coherent pattern in their dustbathing whereas birds that perform sham dustbathing show a more irregular pattern. This suggests that birds which perform sham dustbathing may be frustrated and when birds are given access to peat most will quickly use this for their dustbathing and acquire a coherent dustbathing pattern. Hence, birds can change how they perform dustbathing after they have developed this behaviour. However, birds losing access to peat seemed to be more negatively affected by having to dustbathe without litter than birds which had never experienced litter. Quantifying motivation to dustbathe using a push-door showed that birds which have been reared without peat are motivated to get access to this even after having dustbathed only once in this substrate. The motivation to get access to peat by birds reared without litter was as high as for birds which had always dustbathed in peat. This shows that it is important for birds to perform functional dustbaths even if they have only had experience of sham dustbathing during rearing.

Svensk sammanfattning

Inhysningen av värphöns har genomgått stora förändringar i och med övergången från de konventionella burarna till modifierade burar och frigående system. Anledningen till omställningen var att hönsens välfärd blev ifrågasatt då de konventionella burarna var en torftig miljö där hönsen hade små eller inga möjligheter att utföra många av de beteenden som de skulle ha utfört i en mer naturlig miljö. Mycket tyder på att djur har en stor motivation att utföra beteenden som är viktiga för deras fortlevnad, även om de inte är viktiga för djurens överlevnad i fångenskap, och därför finns det nu krav på att höns ska ha tillgång till sittpinnar, sandbad och rede. De nya systemen som tillgodoser dessa resurser har potential att förbättra välfärden för hönsen, men de är inte problemfria och det är viktigt att djuren kan utnyttja de resurser som finns. Det finns många olika faktorer som kan påverka hur bra fåglar anpassar sig till ett system, men en väldigt viktig aspekt är uppfödningssmiljön. Vad en höna lär sig som liten kyckling kan ha effekter på hur hon betar sig också som vuxen. Bland annat vet man att det är viktigt att kycklingar får tillgång till strö att utföra födosöksbeteenden i för att motverka att de börjar utveckla fjäderhackning. I stora frigående system som är byggda i flera våningar är det viktigt att hönsen hittar upp till de olika nivåerna där reden, mat och vatten finns. Studier har visat att höns som har tidig tillgång till sittpinnar har fördel av detta som vuxna genom att de är bra på att utnyttja de olika nivåerna. Detta har påvisats bland annat av att höns uppfödda med sittpinne är bättre på att lägga sina ägg i upphöjda reden istället för på golvet och att kannibalism förekommer i mindre utsträckning. Om en höna utsätts för en kannibalistisk attack är hon bättre på att fly upp på en sittpinne om hon tidigt har använt pinnar. Trots att det är viktigt för hönsen att använda sittpinnar kan det dock finnas individuell variation i hur bra höns lär sig att göra detta. Därför var syftet med första delen av den här avhandlingen att undersöka om det fanns skillnader i beteendet mellan kycklingar som börjar använda sittpinnar tidigt jämfört med kycklingar som är senare med att börja använda sittpinnar. Dessutom undersöktes sambandet mellan individuell spatial förmåga och användning av sittpinnar med speciellt fokus på om en kyckling till största delen kläcks med en bra spatial förmåga eller om denna till största delen utvecklas genom användning av sittpinnar. Den andra delen av avhandlingen undersökte hur tillgång till ett substrat lämpligt för sandbadning (torv) påverkar utvecklingen av hur kycklingarna sandbadar. Torv är det strömedel som höns tidigare har visat att de föredrar att sandbada i jämfört med exempelvis halm och sågspån. Sandbadning utförs naturligt av höns i ett torrt substrat med små partiklar som kan nå in i fjäderdräkten. Dessa partiklar skakas sedan bort och tar då med sig överflödiga fetter vilket hjälper till att hålla fjäderdräkten i bra kondition med isolerande- och vattenavvisande förmåga. Höns som inte har tillgång till strö utför ändå typiska sandbadnings rörelser och det har diskuterats huruvida hönsens behov av att utföra sandbadning kan bli tillgodosett av att utföra tomgångssandbadning som inte har någon praktisk effekt. Ett syfte med den här studien var därför att undersöka skillnader i hur fåglar sandbadar beroende på om de har tillgång till torv eller inte och hur detta påverkades av om de hade haft tillgång till torv under de första sex veckorna i livet. Dessutom undersöktes också hur erfarenhet att sandbada i torv

respektive tomgångssandbadning påverkade hönsens motivation att sandbada i torv.

För att studera när och hur kycklingar börjar använda sittpinnar följde vi 90 kycklingar som hade tillgång till sittpinnar från kläckning. Observationer av kycklingarnas utnyttjande av sittpinnar och andra beteenden gjordes flera gånger under dagen de flesta dagarna från dag fem till och med att de var sex veckor gamla (Artikel I). Dessa observationer på den individuella användningen av sittpinnar jämfördes med hur kycklingarna löste två olika spatiala test, ett omvägsproblem (detour test) när de var några dagar gamla och hur de orienterade i en åttaarmad labyrint (radial maze) när de var 16 veckor. Därefter gjordes en uppföljning av hur hönsen som vuxna använde sittpinnarna när de flyttades till nya större boxar där de hade tillgång till sittpinnar på flera olika höjder (Artikel II).

Resultaten av studierna av användningen av sittpinnar visade att alla kycklingarna utom en började använda dessa under de första sex veckorna och att det fanns vissa samband mellan kycklingarnas beteende och när de började använda pinnarna. Det fanns indikationer på ett samband mellan ett mer utforskande beteende och tidig sittpinneanvändning då kycklingar som tillbringade mer tid under sittpinnarna under de första veckorna också var snabbare med att använda dessa. Det visades också på ett samband mellan hönsens orienteringsförmåga i den åttaarmade labyrinten vid 16 veckors ålder (tvådimensionell spatial förmåga) och hur mycket de använde sittpinnar när de först sattes in i de nya boxarna (tredimensionell spatial förmåga). Däremot hittades inga samband mellan hur de som små kycklingar använde sittpinnarna och hur bra de var på att lösa omvägsproblemet eller hur de orienterade i den åttaarmade labyrinten. Detta gör att inga slutsatser kunde dras om hur mycket av den spatiala förmågan som är medfödd respektive inlärd.

För att undersöka om utförandet av kycklingarnas sandbadning var beroende av om de hade tillgång till strö eller inte under perioden när de börjar sandbada så föddes 48 kycklingar upp antingen med eller utan tillgång till torv. Fyra olika behandlingar användes avseende tiden kycklingarna fick tillgång till torv; (1) alltid, (2) upp till ca sex veckors ålder, (3) från ca sex veckors ålder och (4) aldrig. När kycklingarna var ca sex veckor gamla och behandling 2 och 3 infördes så videofilmades alla kycklingarna under sex dagars tid. Vid 16 veckors ålder filmades hönsen ytterligare en gång under sex dagar för analys av långtidseffekten av behandlingarna. Från videofilmerna gjordes observationer av när, var och hur mycket djuren sandbadade (Artikel III). Därefter undersöktes om hönsens motivation att sandbada i torv var beroende av deras tidigare erfarenhet av torv (Artikel IV). De höns som fram till nu hade haft tillgång till torv blev av med den och istället fick alla hönsen möjlighet att sandbada i torv i samband med att de testades. Detta gjordes var femte dag och för att komma till en låda med torv var hönsen tvungna att trycka sig genom en svängdörr (push-door). Motståndet i dörren ökades med en Newton från en testgång till nästa om hönan gått igenom föregående gång. Testningen avslutades när en höna inte gick igenom dörren i ett test och det högsta motstånd hon gått igenom användes som ett mått på hur motiverad hon var att sandbada i torv.

Studierna av hur kycklingarna sandbadade visade att kycklingarna förändrade sitt mönster i hur de utförde sandbadning beroende på om det utfördes i torv eller inte. De som inte hade tillgång till torv visade ett mer oregelbundet sandbadningsbeteende med större variation i längden på ett sandbad jämfört med de som sandbadade i torv som hade mindre variation i hur länge de sandbadade. Det fanns indikationer på att det inte var avgörande för hur fåglarna utförde sandbad senare i livet om de som kyckling lärt sig att sandbada i torv eller inte, utan de anpassade beteendet efter om det kunde utföras i ett funktionellt substrat. Hönsen var motiverade att gå igenom svängdörren för att sandbada i lådan med torv och det var ingen skillnad i motivationen mellan höns från olika behandlingar.

Sammanfattningsvis så pekar resultaten på att det finns ett samband mellan tvådimensionell spatial förmåga och tredimensionell spatial förmåga och mellan tidig användning av sittpinnar och ett mer utforskande beteende. Fåglarna kunde ändra sitt sandbadningsbeteende beroende av om de fick funktionell återkoppling eller inte och det var av mindre betydelse om de hade utvecklat sitt sandbadningsbeteende med eller utan torv. Det faktum att alla de vuxna hönsen var motiverade att få sandbada i torv, oberoende av om de hade lärt sig att sandbada i torv eller inte, tyder på att höns har ett stort behov av att få utföra ”riktig” sandbadning och att tomgångssandbadning inte kan ersätta detta.

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