

# **Motivation in Laying Hens**

## **Studies of perching and dustbathing behaviour**

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Knowing you don't know is wholeness.  
Thinking you know is a disease.  
Only by recognizing that you have an illness  
can you move to seek a cure.

Tao Te Ching (translation: J. H. McDonald)

To my family in both ends of Europe



# Abstract

Olsson, I.A.S. Motivation in Laying Hens: Studies of perching and dustbathing behaviour. Doctoral thesis.

Concern for animal welfare has led to changes in legislation and the development of alternative housing systems for laying hens. Perching, dustbathing and nesting have been identified as important behaviours, and the aim has been to develop systems in which the hens can satisfy their motivation to perform these behaviours. In order to reach this goal, knowledge about how motivation to perform different behaviours is regulated is crucial. The aim with this thesis was to extend the knowledge about perching motivation and to study the effect of social factors on dustbathing motivation, with special focus on modified cages where access to the dustbath is limited.

Roosting behaviour at night was studied when hens had free access to perches and when access to perches was thwarted. The findings that hens perch tightly together and that they show signs of unrest when they cannot perch suggest that hens are motivated to perch. This was confirmed in a second experiment where it was found that hens work by pushing open weighted doors for access to a perch.

Social effects on dustbathing motivation were studied by first thwarting hens of dustbathing in the presence of stimulus hens either dustbathing or not dustbathing and then giving the test hens access to litter. No effect of the behaviour of the stimulus hens on test hens' dustbathing behaviour in litter was found, suggesting that social facilitation is of little importance for dustbathing motivation.

Dustbaths are provided in modified cages since it is known that birds are motivated to dustbathe but, despite this, sham dustbathing is frequent. To investigate reasons for this, the background of sham dustbathing was investigated in three experiments. The results from the first two experiments indicated that performing sham dustbathing does not reduce motivation to dustbathe in litter and that sham dustbathing, like normal dustbathing, is not affected by social facilitation. But the results from the third experiment suggest that previous experience affects the performance of sham dustbathing. This may have implications for how birds are reared for this system and when they get access to the dustbaths in modified cages.

Keywords: animal welfare, behavioural need, operant technique, *Gallus gallus domesticus*, fowl, poultry



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I. Olsson, I.A.S. and Keeling, L.J. 2000. Night-time roosting in laying hens and the effect of thwarting access to perches. *Applied Animal Behaviour Science*, 68:243-256.

II. Olsson, I.A.S. and Keeling, L.J. The push-door for measuring motivation in hens: Laying hens are motivated to perch at night. *Animal Welfare*. Accepted for publication.

III. Olsson I.A.S., Duncan, I.J.H., Keeling, L.J. and Widowski, T.M. How important is social facilitation for dustbathing motivation in laying hens? Manuscript.

IV. Olsson, I.A.S., Keeling L.J. and Duncan, I.J.H. Why do hens sham dustbathe when they have litter? The background to sham dustbathing in modified cages. Submitted.

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## Introduction

In the first half of the 20<sup>th</sup> century, egg production in Sweden was based on small flocks of hens kept in extensive housing systems with a henhouse and an outdoor area. Any countryside house would have a flock of hens and eggs were an important source of protein in the diet, easily available every day on the farm. Looking after the hens was the woman's responsibility and through selling eggs she could get some cash income of her own. During the second half of the century, this type of subsistence farming was replaced by large-scale agricultural production. Animal husbandry became animal production and this also affected the housing of hens. The battery cage allowed automatization of feeding, egg collection and manure disposal, so that one person could look after many more hens than in a free-range or loose-housing system. An additional advantage was that stocking density per floor area of the building could be increased. As a consequence, battery caged hens in production units of several thousand hens became the predominant form of production during the 1960s and 1970s.

The development of intensive animal production met criticisms from the general public. The discussion about animal welfare in modern agriculture was sparked by the publication of Ruth Harrison's book "Animal Machines" in Britain in 1964. The debate spread over Western Europe and animal welfare science was for the first time used as a basis for political decisions in 1965 when the British government set up a scientific committee, known as the Brambell committee, to investigate the welfare of farm animals. In order to draw conclusions about animal welfare, scientists study how animals react, behave and function in different situations. Some animal welfare scientists place the emphasis on the health and biological functioning whereas others say animal welfare has primarily to do with the feelings of animals. The concept of animal welfare has been extensively discussed elsewhere (*e. g.* Sandøe & Hurnik, 1996; Duncan & Fraser, 1997) and rather than engaging in this discussion here, I want to underline that the difference in emphasis need not imply such a lack of agreement as first appears. In most cases it can be assumed that an animal which is healthy is also feeling well and that a diseased animal is feeling bad. To avoid the problem with marginal cases which fall outside one of the definitions and inside the other, it could be said that animal welfare is to do both with the state of animals and what they feel. Moreover, one reason to engage in the study of animal welfare is the combination of that animals are able to have negative or positive feelings and that society and scientists attribute importance to these feelings. Scientists in animal welfare use knowledge about the biology and species-specific behaviour of animals to make predictions about how systems should be designed in order to promote good welfare. Animal welfare has been a growing field of science during the last 35 years, and research results have been increasingly important as the basis for legislation.

In combination, research results and the growing public concern for the welfare of hens in battery cages has led to the call for alternative housing systems. Small-scale backyard hen keeping, which is often seen as the public's ideal, is not without welfare problems. Either freely roaming around or kept in houses with an outdoor area, the hens are exposed to diseases and parasites and also threatened by predators. But from the behaviour point of view, this system has an obvious advantage in that it is not very restrictive and allows the hens to express most of their behavioural repertoire. As a contrast, in the standard battery cage for laying hens, many natural behaviour patterns are prevented and it is generally believed that such restricted environments give rise to animal welfare problems (see Petherick & Rushen, 1997). One way to alleviate the problems with behavioural restriction is to return to loose-housing systems. Various systems for large flocks, such as aviaries, free-range systems and deep litter pens, have been developed in order to adapt the unrestricted housing system to large-scale production. An alternative line of work has been to identify key behaviours for the hens and incorporate those within the cage, leading to what is now known as modified cages. For both systems, economic constraints call for minimum space utilisation at the same time as the requirements of animal welfare legislation must be met. Under these conditions, knowledge about hens' behaviour is essential to combine economically profitable production with acceptable welfare.

## **Motivation**

In intensive housing systems, animals are prevented from performing many of the behaviours they would perform under more natural conditions. The potential problem with this restriction was first recognised by scientists in the Brambell committee, stating that animals possess "behavioural urges" which could be frustrated (see Hughes & Duncan, 1988). Initially, attempts were made to define which behaviours should be considered 'ethological needs', but this approach was heavily criticised in Marian Dawkins' influential paper "Battery hens name their price: Consumer demand theory and the measurement of ethological 'needs'" (1983). Instead Dawkins advocated that research should focus on motivation. This is a collective term for the factors which make animals behave in a certain way, and motivation has been a central concept in animal welfare research since the publication of Dawkins' paper. Although the idea of behavioural needs has not disappeared from animal welfare theory, in later definitions it has been based on the concept of motivation (see Petherick & Rushen, 1997) and it is assumed that the welfare of an animal will be reduced if it cannot perform behaviours for which it is motivated (Hughes & Duncan, 1988; Jensen & Toates, 1993). Restricting behaviour will most likely affect welfare if the motivation arises from internal factors, if motivation remains high when the behaviour cannot be performed and if motivation is reduced by performing the behaviour rather than achieving the consequences (Petherick & Rushen, 1997).

### *Evolutionary aspects of motivation and welfare*

Through natural selection, behavioural mechanisms have evolved in such a way that survival is enhanced under natural conditions. A system of positive and negative experiences ensures that the appropriate action is taken. That is, behaviours increasing fitness are perceived as rewarding whereas those associated with reduced fitness are aversive (Dawkins, 1990,1998; Broom, 1998). It has been suggested that this system of reinforcers operates independently of the fitness consequences. So even in a captive environment, where the physical danger has been removed, a situation that in nature would constitute a threat to survival will still be perceived as aversive by the animal (Dawkins, 1998). But even having said that, this does not mean that all behaviours for which an animal is motivated in nature are important also in captivity. What is important is that the animal can perform a certain behaviour if it is motivated to do so, that is if the factors which increase the tendency to perform the behaviour are present.

### *Social effects on motivation*

In group-living animals such as the domestic hen, other members of the group have an influence on behaviour and motivation. Clayton (1978) defined three different ways in which social factors can influence motivation. In the case of *social inhibition*, the presence of other individuals inhibits the performance of certain behaviour patterns. The opposite, defined as *solitary inhibition* can also be found, when certain behaviours are only performed in a social context and thus are inhibited in a solitary individual. Finally, *social facilitation* acts when an animal starts performing a behaviour or increases the intensity when it sees another individual performing the behaviour. An important consequence of social facilitation is synchronisation of behaviour, *i. e.* that members of a flock are engaged in the same behaviour at the same time. This enhances the adaptive aspects of group living, such as protection from predators (Lazarus, 1972; Clayton, 1978). In the wild, hens are group-living and synchronisation of behaviour is found even in domestic hens in cages (Webster & Hurnik, 1994).

### *Measuring motivation*

Several methods are available for experimental studies of motivation, such as preference studies, consumer-demand studies, and studies of deprivation/frustration (see Fraser & Matthews, 1997 for a review). In preference studies the animals are given the choice between different resources, and the time spent with the different alternatives is measured (Dawkins, 1990; Foster *et al.*, 1997; Fraser & Matthews, 1997). Such studies give information about animals' preferences, but this is not sufficient to draw conclusions for animal welfare. Preference studies therefore need to be combined with some kind of measure of motivational strength, to establish how strongly an animal prefers (or wants to avoid) a certain option. Consumer demand theory has been applied to serve as this measure, estimating the motivational strength from the 'price' the animal is willing to pay to get access to the resource. The higher the price the animal is prepared to pay, the higher the motivation (*e. g.* Dawkins, 1990, 1998; Fraser &

Matthews, 1997). However, the application of economic theory on welfare research is not unambiguous and in a critical review, Mason *et al.* (1998) gave guidelines for such experiments. According to these guidelines, animals should be tested in closed economies where the resource is not available outside the test situation. It is also important that the costs are perceived equivalently for different resources and that the animals are allowed to perform complete behaviour patterns without interruption.

Another way to study motivation is to deprive the animal of the possibility to perform the behaviour and see how this affects behaviour. If the behaviour is one that the animal is motivated to perform, it will respond with behavioural changes. Changes may occur during the deprivation, such as the performance of vacuum activities (showing the behaviour despite the lack of external stimuli) or displacement activities and abnormal behaviour (Dawkins, 1990; Mench & Mason, 1997). If the animal is first prevented from performing a behaviour for which it is motivated and the possibility to perform the behaviour is then returned, a rebound effect may be found. That is, the animal will initially spend more time performing the behaviour than before the period of deprivation (Dawkins, 1988, 1990). An increase of exploratory behaviour, during which the animal is thought to look for a possibility to perform the thwarted behaviour, may also be seen (Nicol & Guilford, 1991).

A number of different techniques have been used for measuring motivation in poultry. In a series of experiments, Duncan and Wood-Gush (1971, 1972) thwarted feeding behaviour and studied the hens' reaction to this frustration. By depriving hens for a long time and then studying the rebound at renewed access to litter, van Lier and Wiepkema (1992) investigated hens' motivation for dustbathing. Nicol and Guilford (1991) estimated motivation by the amount of exploratory behaviour performed by hens deprived of food or litter. In later experiments, operant techniques have been predominant and various different methods have been used, such as: key-pecks (litter: Dawkins & Beardsley, 1986; Matthews *et al.*, 1995), a weighted push-door (nest: Follensbee *et al.*, 1992; litter: Widowski & Duncan, 2000), squeezing through a narrow doorway (nest: Cooper & Appleby, 1995, 1996, 1997) or passing an unfamiliar or higher-ranked conspecific (nest: Freire *et al.*, 1997) and exposure to draught while using the resource (litter: Faure & Lagadic, 1994).

## What is important to the hen?

Taking into account the problems with behavioural restriction for hens in battery cages, it has been suggested that certain resources should be provided in order to allow important behaviours to be performed. It was also suggested that these resources should be specified in animal welfare legislation (Appleby, 1993). This is in fact reflected in present European Union (EU) legislation, which states that housing systems for laying hens should provide nests, litter and perches (European Union, 1999). The choice of these resources is based on what is known about hens' behaviour and resource use.

### *Perching*

Under natural conditions, a flock of chickens return each night to the same preferred roosting site where they spend the night perching on branches of trees (McBride *et al.*, 1969; Wood-Gush *et al.*, 1978). By resting in an elevated location, birds are protected from ground predators and the foliage of the tree gives protection from above. Roosting together can also help to conserve heat. The afternoon light decreasing below a certain intensity is the cue for going to roost (Kent *et al.*, 1997). When hens have access to perches in commercial housing systems, the majority of birds use perches for roosting at night (Duncan *et al.*, 1992; Appleby *et al.*, 1992, 1993; Appleby, 1995; Abrahamsson, 1996).

When housed in high-density aviary systems, birds reared with perches laid fewer floor eggs and had fewer problems with cannibalism than birds which had got access to perches only after the age of 4 weeks (Gunnarsson *et al.*, 1999). Access to perches has implications for bird welfare also in cages, where the inclusion of perches has resulted in increased bone strength (Duncan *et al.*, 1992; Abrahamsson, 1996). The design of the perch has effects on foot health and keel bone deformation (Abrahamsson, 1996). Preferences have been found for higher perches over lower (Keeling, 1997), but not for perch shape (Lambe & Scott, 1998).

### *Dustbathing*

Hens dustbathe in loose material, such as sand or earth. A dustbathing hen squats down in the substrate and works the substrate into her plumage following an organised sequence of behaviour patterns. The behaviour is part of plumage maintenance, removing stale and excess lipids (van Liere, 1992). Adult birds with access to litter dustbathe about every second day (Vestergaard, 1982).

Following a period of litter deprivation, hens show a rebound in dustbathing behaviour when they are given access to litter (Vestergaard, 1982; van Liere & Wiepkema, 1992). According to the model by Hogan and Van Boxel (1993), dustbathing behaviour is regulated through an internal motivation building up with time since last dustbathing, together with an effect of external light and heat

which lowers the threshold for the behaviour. Social facilitation is also believed to play a role in dustbathing motivation (Vestergaard, 1981b; Duncan *et al.*, 1998). Hens have been shown to work for access to litter (Matthews *et al.*, 1995; Gunnarsson *et al.*, 2000a; Widowski & Duncan, 2000).

If hens are kept without litter sufficiently long, they develop sham dustbathing behaviour, which is when they go through the sequence of dustbathing but on the bare floor (Vestergaard, 1981a,b; Appleby *et al.*, 1993; Petherick *et al.*, 1995). Vestergaard *et al.* (1990) found that in chicks reared without litter, the pattern of sham dustbathing develops in a way similar to that of normal dustbathing in chicks reared with litter. Sham dustbathing such as in litter-deprived hens has also been seen in hens kept in modified cages with a dustbath (Lindberg & Nicol, 1997).

#### *Foraging in litter*

Besides dustbathing, hens also peck and scratch in litter (Bubier, 1996a,b; Hughes & Channing, 1998) as part of their foraging behaviour. Such foraging makes up the majority of the active period in junglefowl, and this fact has been taken as an indication that restricting this behaviour has negative consequences for welfare (Dawkins, 1989).

#### *Nesting*

Hens show a distinct nesting behaviour pattern which starts 1-2 hours before oviposition and is regulated through a series of endocrine events following ovulation (see Petherick & Rushen, 1997). Under unrestricted conditions, hens move away from the flock before laying, seeking out a protected location for the nest (Duncan *et al.*, 1978). Operant studies indicate that domestic hens are motivated to lay in a nest (Follensbee *et al.*, 1992; Cooper & Appleby, 1995, 1996, 1997). This motivation is present already when a hen lays her first egg, before she has any experience of nesting (Cooper & Appleby, 1995). When hens are kept in cages without a nest box, signs of frustration can be seen at the time of oviposition (Duncan, 1970).

## **A housing system satisfying hens' needs**

The standard battery cage for laying hens is a very restricted environment, which prevents the hens from performing many natural behaviour patterns, such as resting in the natural, perching position, laying in a secluded location and dustbathing and scratching in litter. In the light of the indications of frustration and sham behaviours, hen welfare is likely to be compromised in battery cages. Alternatives such as loose-housing systems and modified cages have been developed as an attempt to meet this problem. In loose-housing systems, large flocks of hens are housed together in big areas where litter, nests and perches are provided along with food and water. In modified cages, the main features of the battery cage are retained but the area and complexity is increased by including a nest, a dustbath and a perch. In both systems, the hens are kept in groups. Whereas competition for resources is less of a problem in loose-housing systems, limited space in nests and dustbaths in modified cages may lead to competition if several birds are motivated to use the resources at the same time. This competition may be further aggravated by social facilitation. An extensive knowledge about motivation for different behaviours and how it is affected by social factors is necessary to ensure functioning of these alternative housing systems.

## Aims

With the background of the recent development of modified cages and legislation prescribing access to litter, nests and perches, there is a need for increased knowledge about the control of motivation for using these resources. Previous research has focused on motivation for dustbathing and nesting, whereas the motivation for perching has not been studied. Furthermore, the effect of social factors on motivation has received little attention. Therefore, the work in this thesis is concentrated on these two aspects of motivation. More specifically, the aims were:

To study the effect on behaviour of thwarting access to perches for night-time roosting.

To quantify hens' motivation for night-time perching and study how this is affected by social stimuli

To study how social stimuli, *i. e.* the presence of other dustbathing hens, affect dustbathing motivation

To study the motivational background of sham dustbathing behaviour: the effect of sham dustbathing on motivation for dustbathing in litter as well as the effect of social facilitation and of habit on sham dustbathing.

## Materials and methods

The papers in this thesis consist of more than one experiment and the following section gives an overview of the different experiments contained in each paper.

In Paper I, night-time roosting and the effect of thwarting access to perches was studied. The same hens were tested in two experiments:

1. A study of night-time roosting under undisturbed conditions in the home pen
2. A study of behaviour when access to perches was thwarted in experimental pens.



In Paper II, the motivation for night-time roosting and the effect of social factors on this motivation was studied. The same hens were tested in two experiments:

1. A study of behaviour and push-door resistance opened in an experimental pen where opening the push-door gave access to either a perch or, as a control, a structure where perching was not possible
2. As above but with the resources being either a perch with a perching companion hen or, as a control, a perch with a companion hen on the floor.

In Paper III, the effect of social facilitation on dustbathing behaviour was studied. The same hens were tested in two experiments where dustbathing was thwarted in the presence of stimulus hens and where test hens were thereafter given access to litter:

1. A study of behaviour when pairs of test hens, either deprived or not deprived of litter, were exposed to pairs of stimulus hens dustbathing or not dustbathing on litter
2. A study of behaviour when individual test hens were exposed to individual hens dustbathing or not dustbathing on litter and thereafter allowed to join the stimulus hen on litter.

In Paper IV, the effects of sham dustbathing on dustbathing motivation was studied as well as the effect of social stimuli and of habit on sham dustbathing behaviour. Two different sets of hens were studied, one in the first experiment and another in the second and third experiments.

1. A study of behaviour when litter-deprived hens were tested in a situation where they could either dustbathe in litter, sham dustbathe or not dustbathe at all and were thereafter given access to litter.
2. A study of behaviour when litter-deprived hens were exposed to the stimulus of other hens with or without litter and either dustbathing or not dustbathing.
3. A study of behaviour when hens deprived of litter for a long time were again given access to litter.

## **Animals and husbandry**

In papers I and II, hens of the hybrid Lohmann Selected Leghorn (LSL) were studied. The birds had been commercially reared in a floor system with access to perches and they were housed in floor pens with litter (wood-shavings), nests and perches during the experiment.

In paper III, hens of the hybrid Black Dekalb were studied in the first experiment, whereas Lohmann Brown hens (LB) were used in both the second and third experiments. The Black Dekalb hens used in experiment 1 had been commercially reared in a floor system and were beak-trimmed. During the experiment, the hens were housed in wire-floor pens with access to low perches and a nestbox. An arrangement of rods was placed over the floor to prevent birds

from sham dustbathing. The LB hens used in experiment 2 and 3 had been commercially reared on litter, and prior to the experiment they were housed in groups of five in floor pens with litter, perches and nests. During the experiment they were housed in a group in a floor pen (wire-floor and concrete) with access to perches and nests. The hens were housed without litter for dustbathing but were given straw in which they could forage.

In paper IV, the same birds were studied as in the first experiment in paper III: beak trimmed Black Dekalb, commercially reared on litter floor. During the experiment, the birds were housed in pens with low perches. During periods of litter deprivation, pens with wire floor were used, but birds had access to litter (wood-shavings and peat moss) every third day.

Food and water were available *ad libitum* to all birds.

## Methods

Paper I describes two experiments studying night-time roosting. Observations took place mainly during the dark period, in the weak light of dimmed spotlights which made it possible to see the white hens. In experiment 1, night-time roosting in the home pen was studied. Two groups of 26 hens each were studied in their home pens, where they were provided with ample perching space at three different heights. Behaviour was directly observed during 60 minutes from lights-off and the number of hens at each perch level was counted at regular intervals. In experiment 2, behaviour was studied when perching at night was thwarted, with and without the perch being visible. Groups of three hens were placed in small pens with access to perches similar to those in their home pens in experiment 1, and allowed a one-week adaptation period before the observations started. The hens were observed during four consecutive days in the following treatments; pen unchanged, perch covered with plexi-glass, perch removed and again pen unchanged. The order of the two middle treatments in which perching was thwarted was balanced over the groups of hens. The birds were observed during 15 minutes before lights-off and subsequently during the first 60 minutes of the dark period. Behaviour and location of birds was recorded as continuous observations of focal birds and registered using a handheld computer and the Observer software.

The experiments described in paper II were based on the push-door technique, which was modified to use fixed levels of resistance, individually adapted to each hen's capacity. The push-door was a swing-door, hinged at the top, and held closed by an electromagnet. The bird could see through the door to the other side and open it by putting her head through the centre opening and pushing with the front of her wings (see Figure 1). The hens were trained to push through the door using food as the resource, and the individual capacity of each hen was determined by exposing a hen to increasing resistances in daily trials during

subsequent days, until she did not open the door. In the experiments, the resource was placed on the other side of the push-door and the hens (N=8) were tested with two series of increasing resistances. Each series lasted six days; the first two with no resistance and thereafter 25, 50, 75 and 100 % of individual maximum. The maximum resistance opened was recorded. Furthermore, for each resistance the latency to contact with the door, latency to open and number of attempts to open were recorded. Following the standard practice from operant experiments, only results from the second series of resistances were used. The push-door was used in experiment 1 to measure motivation for a perch for night-time roosting and in experiment 2 to study how this motivation was affected by the presence of a companion hen. The hens were tested in an experimental pen with two compartments, separated by a netting wall in which the push-door was inserted. At lights-off the hens were released into the start compartment, and by pushing through the door could reach the resource compartment. In experiment 1, this compartment contained either a perch or, as the control, a sham perch covered by an inclining board which prevented hens from perching on it. In experiment 2, the resource compartment contained either a perch with another hen perching or, as the control, a perch with another hen on the floor. Behaviour was recorded from video recordings in experiment 1 and through direct observations in experiment 2.

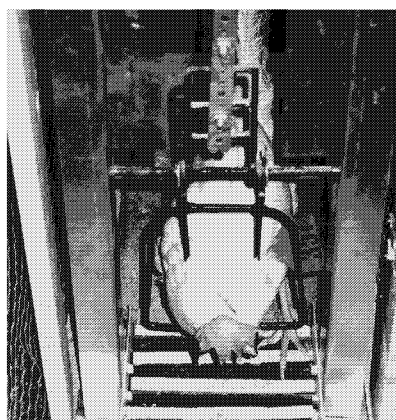


Figure 1. The push-door used for measuring motivation for perching in paper II.

Paper III presents two experiments investigating the possible effect of social facilitation on dustbathing motivation. The hens were tested in an experimental pen consisting of two parts divided by plexi-glass; one compartment had a wire floor whereas the other contained a layer of peat moss. Hens to be tested were placed on the wire floor side and stimulus hens, familiar to the test hens, were placed on the peat side. The plexi-glass separating the two compartments allowed hens to see each other. The stimulus consisted of stimulus hens either dustbathing or not dustbathing, and was controlled by previous litter deprivation of the

stimulus hens. In experiment 1, twelve pairs of test hens were tested together with pairs of stimulus hens. The hens were tested both deprived and non-deprived. When deprived, they had been housed without litter for 70 h and when non-deprived, they had been housed with litter 22 h previous to the experiment. They were tested in three treatments: stimulus hens dustbathing in peat, stimulus hens on peat but *not* dustbathing and peat only but no stimulus hens. The stimulus period lasted 30 minutes, after which the stimulus hens were removed and the test hens lifted over to the litter compartment. In experiment 2, twelve single hens were tested with single stimulus hens. The test hens were deprived of litter 24 h prior to the test and were tested in two treatments: stimulus hen dustbathing in peat and stimulus hen on peat but not dustbathing. After the hen had been exposed to the stimulus for 7 minutes, she was allowed to enter the litter compartment, with the stimulus hen still present, and allowed to dustbathe there until both birds had stopped dustbathing. If birds were still dustbathing after 75 minutes on litter, this dustbathing was interrupted and birds were returned to the home pen. In both experiments, behaviour of the hens was registered both during the stimulus period and during the subsequent access to litter. Behaviour was video recorded and analysed using the Observer software, except for the recordings during litter access in experiment 2, which were performed as direct observations.

Paper IV describes three experiments in which sham dustbathing was studied. In experiment 1, the effect of performing sham dustbathing on dustbathing motivation was studied. Twenty-four hens were deprived of litter for eight weeks and thereafter tested for the performance of sham dustbathing. Twelve pairs of hens were formed of which at least one hen had shown sham dustbathing. All hens were then given access to peat moss before the experiment started. Pairs of hens were tested in experimental pens where the hens were first given one of three treatments for 60 minutes and thereafter given access to peat moss for 75 minutes. The treatments were a wire floor over a peat covered concrete floor where sham dustbathing was possible (experimental treatment), the same wire floor but with a horizontal grid preventing sham dustbathing (negative control) or the peat covered concrete floor only (positive control). Behaviour during treatment and during subsequent litter access was recorded on video and analysed with the Observer software. In experiment 2, the effect of social stimuli on sham dustbathing was studied. Twelve hens deprived of litter for ten weeks were tested individually. The test hens were tested together with pairs of familiar stimulus hens in an experimental apparatus consisting of a two-compartment pen with a netting wall separating the two compartments. In the stimulus hen compartment the concrete floor was covered with a mix of peat and sawdust whereas in the test hen compartment, half of the concrete floor area was bare and the other half had a raised netting floor placed over it. The hens were tested with three different treatments: stimulus hens dustbathing on litter, stimulus hens not dustbathing but with litter present and stimulus hens without litter. The hens were exposed to the stimulus for a minimum of 45 minutes in the test pen. Additionally, in treatment 1

hens were tested for at least 30 minutes during which stimulus hens were dustbathing. Before tests, hens were prevented from sham dustbathing during two days. Behaviour was observed directly, during continuous observations altering between two hens tested simultaneously. In experiment 3, the effect of habit on sham dustbathing was tested. After 12 weeks of litter deprivation, a group of 26 hens (the same as in experiment 2) was given access to litter in their home pen. Their behaviour 6 to 7 hours after lights-on, which is the presumed diurnal peak of dustbathing motivation, was studied by direct observation of dustbathing and sham dustbathing behaviour using scan sampling.

## **Statistics**

The statistical analyses are described in detail in the separate papers. Whenever possible, a within-subject design was used and the data were analysed with Wilcoxon Matched Pairs Signed Rank Test, with corrections for multiple comparisons where appropriate.

## **Results**

In paper I, night-time roosting behaviour was studied. In experiment 1 it was found that as soon as the lights went off, birds started to go up onto the perch. Starting from the lowest perch, the hens jumped further up from perch to perch. The birds perched close together, and hens who got an end position were frequently seen trying to move to the centre, pushing other hens out of place. After about 10 minutes all birds were settled on the top perch, where they perched tightly together leaving about one fourth of the perch length empty. No hens roosted on lower perches or other locations in the pen. In experiment 2, no treatment differences were found before the start of the dark period. During the dark period, when the perch was available, birds went up onto it almost immediately and remained roosting throughout the observation. When no perch was available, the hens spent most of the time on the floor, although part of the time was spent also in the nest. They spent less time sitting ( $p=0.042$ ) and tended to spend more time standing ( $p=0.06$ ) and they walked more ( $p=0.042$ ) when no perch was available. However, towards the end of the observation hour, walking decreased and time sitting increased also when birds had no access to the perch.

In paper II, motivation for night-time roosting was measured using the push-door. In experiment 1, it was found that most hens opened the door for access to the perch whereas only one hen opened it in the control situation. Thus, the hens opened doors at heavier resistances in the treatment with a perch than in the control treatment ( $p=0.018$ ). Few hens opened the door in the control treatment, and so most hens scored the maximum latency to contact and correspondingly zero attempts to open. As a consequence, the statistical comparison revealed

shorter latencies to contact in the treatment with the perch than in the control (for the different resistances 25-100 % of individual maximum: 25%  $p=0.071$ ; 50%  $p=0.03$ ; 75%  $p=0.03$ ; 100 %  $p=0.053$ ) and similarly fewer attempts to open the door (25%  $p=0.03$ ; 50%  $p=0.018$ ; 75%  $p=0.018$ ; 100 %  $p=0.03$ ). During the continued observation throughout the dark period, hens with access to a perch changed position more often than those without a perch ( $p=0.035$ ) but no difference was found in the time spent sitting and standing. In experiment 2, where the effect of a perching companion hen was studied, only four hens opened the door and no treatment effect was found on any of the variables measured.

In paper III, the effect of social stimuli on dustbathing motivation was studied. In experiment 1, it was found that birds spent more time closely facing dustbathing stimulus hens than when the stimulus was the litter only, a difference which was significant for deprived hens ( $p=0.006$ ) and a tendency for non-deprived hens ( $p=0.064$ ). Furthermore, the hens walked more in the presence of dustbathing stimulus hens than when no stimulus hens were present (deprived  $p=0.006$ ; non-deprived  $p=0.016$ ). Comparing the two treatments with stimulus hens present, the only effect of whether or not stimulus hens were dustbathing was an increase in walking in the presence of dustbathing stimulus hens when the test hens were deprived ( $p=0.044$ ). Whether birds dustbathed at subsequent access to litter was largely determined by their level of deprivation, as almost all deprived and very few non-deprived hens dustbathed. Neither latency to start dustbathing nor time spent dustbathing was affected by previous stimulus. The post-hoc comparison between observations where both birds dustbathed and observations where none of the birds dustbathed (mainly corresponding with comparisons between deprived and non-deprived birds), revealed that during the stimulus periods birds that would later dustbathe spent significantly more time facing ( $p=0.004$ ) and closely facing ( $p=0.003$ ) the stimulus side, less time preening ( $p=0.031$ ) and walked more ( $p=0.045$ ), and they also tended to show more signs of frustration ( $p=0.065$ ) during the stimulus exposure than did birds which would not dustbathe afterwards. During the stimulus exposure in experiment 2, birds spent less time facing ( $p=0.001$ ) and closely facing ( $p=0.001$ ) the stimulus when the stimulus hen was dustbathing than when she was not dustbathing. More displacement preening was seen when watching a dustbathing than a non-dustbathing stimulus hen ( $p=0.002$ ). Treatment did not affect subsequent dustbathing behaviour on litter, and furthermore no difference was found between observations where both hens were dustbathing together and observations where only one hen was dustbathing.

In paper IV, sham dustbathing was studied in different situations. In experiment 1, when the birds were initially observed during the three treatments, all 24 birds dustbathed in the treatment with litter (the positive control), and no birds showed any dustbathing movements in the treatment with a rod floor (the negative control), whereas seven birds sham dustbathed in the treatment with a wire floor (the experimental treatment). Only these seven sham dustbathers were

included in further analyses. The time spent sham dustbathing in the experimental treatment was significantly shorter than dustbathing in the positive control with litter ( $p=0.044$ ), whereas the latency to start dustbathing (sham or in litter) was longer ( $p=0.044$ ). No differences were found between the experimental treatment and the negative control. When the birds were subsequently given access to litter, all birds dustbathed after the experimental treatment and the negative control, and six birds also dustbathed a second time after the positive control treatment with litter. Birds spent longer time dustbathing after the experimental treatment than after the positive control ( $p=0.044$ ) and the latency to start dustbathing was shorter ( $p=0.044$ ), whereas there were no significant differences between the experimental treatment and the negative control. In experiment 2, six out of eleven birds showed sham dustbathing; three of those sham dustbathed only in the treatment with litter and dustbathing stimulus hens and two only in the treatment with litter and non-dustbathing stimulus hens, whereas one hen sham dustbathed in all three treatments. The number of hens sham dustbathing did not differ significantly between treatments, but when the treatments with litter present were lumped, there was a tendency for more hens to dustbathe when litter was present than when not ( $0.1 > p > 0.05$ ). There was no significant effect of treatment on any of the behavioural variables measured. In experiment 3, four birds were seen sham dustbathing in the concrete aisle the first day with access to litter. The second day, one of these birds sham dustbathed again and two new birds also sham dustbathed. No birds were seen sham dustbathing on the third day of observation. All birds except two were seen dustbathing on litter the first day. These remaining two were not seen bathing in the litter until the third day of observation, and whereas one of them sham dustbathed the second day, the other was not seen sham dustbathing.

## General discussion

This thesis deals with the subject of motivation. It has focused on two different behaviours in laying hens: perching and dustbathing and motivation has been measured using different methods. The results of the studies on perching show that hens are motivated to roost on a perch at night. In the study of dustbathing, it was found that social stimuli have little influence on motivation, implying that dustbathing is not socially facilitated. Sham dustbathing, which has previously been found to occur frequently in modified cages, cannot be explained by an effect of sham dustbathing on dustbathing motivation or by social facilitation. Instead, it is suggested that sham dustbathing is affected by early experience.

## Measuring motivation

The concept of motivation is central in the study of animal welfare, and it is therefore important to have appropriate and accurate methods to measure motivation. Methods generating a demand function are the most common (Mason *et al.* 1998), but such methods are fully appropriate only for commodities which can be bought in discrete quantities at repeated occasions. For commodities such as a perch for night-time roosting, where the resource is meaningful only if access is given until a full behavioural sequence has been completed, methods where the birds pay an 'entrance-fee' to get unlimited access to the resource are more suitable. In the light of this, to measure hens' motivation for night-time perching we used a modified version of the push-door first used by Ian Duncan and further developed by Petherick and Rutter (1990). In our modification of the door, fixed resistance levels are used which are adapted to each individual hen, and in a study with feed-deprived hens and feed as a resource, we have previously found that this modified method is valid for measuring motivation (Olsson *et al.*, accepted). In paper II, this modified push-door technique was successfully applied to measure motivation for night-time roosting.

Besides the push-door, other methods for measuring motivation have been described in this thesis. In paper I (perching) and paper IV (dustbathing), behaviour at behavioural thwarting was studied. In paper IV, the latency to performing a behaviour was also used as a measure of motivation.

## Perching

Feral hens roost on branches of trees and also under commercial conditions hens make frequent use of perches for night-time roosting (Duncan *et al.*, 1992; Appleby *et al.*, 1992,1993; Appleby, 1995; Abrahamsson, 1996). The hens in papers I and II all perched at night when they had access to perches, a finding which is in accordance with previous research. Although there was ample perch space at various levels, all birds perched tightly together on the top perches (paper I). This is consistent with the findings by Blokhuis (1984) who found that most birds rested on the highest perches.

When access to perches was thwarted the hens walked more and took longer to settle than when they could perch (paper I). This, together with the high use of perches, indicates a motivation to perch, which was confirmed in paper II, where it was found that hens work for access to a perch for night-time roosting. This is the first experimental evidence that hens are motivated to perch.

Since birds perch together, it can be expected that social factors have an influence and that birds would be more motivated to perch together than to perch alone. Such an effect on motivation was not found in paper II, where hens did not



work more to perch together with a perching companion than to perch with a companion hen on the floor. However, as reported in paper II, there were methodological problems with this experiment, which calls for caution when interpreting the results. The finding in paper I that hens perched tightly together even though there was more than enough space indicate that they do indeed prefer to roost in contact with each other.

It should be noted that the experiments in paper I and II were carried out with hens who had been reared with perches. The development of perching behaviour is dependent on early access to perches, and if birds are given perches at 8 weeks of age or later they will start to perch only slowly (Appleby & Duncan, 1989). It could be argued that birds reared without perches may not be motivated to use them and hence would not suffer from the absence of perches. Nevertheless, if the birds are given sufficient time or if they are repeatedly lifted up onto the perch (see Gunnarsson *et al.*, 2000b), it seems as if most birds develop perching behaviour even if they have been reared without a perch. Moreover, access to perches affects bird welfare positively by increasing bone strength (Duncan *et al.*, 1992; Abrahamsson, 1996).

## **Social effects on dustbathing**

Hens dustbathe together and the observation that if one hen starts to dustbathe others will join her has led to the suggestion that the behaviour is socially facilitated (Vestergaard, 1981b). However, only recently has the question of possible social facilitation of dustbathing been experimentally studied, by Duncan *et al.* (1998) and Lundberg and Keeling (submitted), and in paper III in this thesis. The results reported in paper III give no support for an effect of social facilitation on dustbathing behaviour. Neither the previous observation of dustbathing birds nor the presence of a dustbathing bird which the test bird could join had any effect on the dustbathing behaviour of test birds.

These results contradict the suggestion of Duncan *et al.* (1998), who found that hens dustbathed more in the presence of dustbathing hens and interpreted these results as the effect of social facilitation. However, as has been pointed out by Lundberg and Keeling (submitted), there are other possible ways in which social factors can affect motivation, such as social inhibition and solitary inhibition, which are sometimes difficult to distinguish between. In the experiment by Duncan *et al.* (1998), the hens were either alone or observing dustbathing stimulus hens, and the possible effect of solitary inhibition in the control situation cannot be separated from that of social facilitation in the experimental treatment. Likewise, Lundberg and Keeling (submitted) give two possible interpretations of their finding that high-ranked hens had a shorter latency to dustbathe when shown a dustbathing hen on video than when shown a standing hen on video. Indeed, this could be social facilitation, but it could also be a type of social inhibition, in which the sight of a standing bird inhibits dustbathing in the test bird. In paper

III, birds were always tested together, either as a pair of test birds or paired with a familiar stimulus bird during the whole test, in order to avoid solitary inhibition. Nevertheless, an effect of the presence of other birds was found, in that birds paid more attention to the stimulus if this was dustbathing hens than if it was a dustbathing substrate only. Since live stimulus hens were used, it is possible that an effect of interaction between test and stimulus birds can have contributed to this.

Although subsequent dustbathing behaviour was not affected, observing dustbathing stimulus birds did affect the behaviour of test birds in paper III. Test birds which had not been deprived of litter walked more when they were watching dustbathing stimulus birds than when they were watching stimulus birds which were not dustbathing. When the test birds were moderately litter deprived they showed more displacement preening in the same situation, possibly indicating frustration at high motivation levels. Thus, irrespective of the role of social facilitation, the results in paper III indicate that the presence of dustbathing hens affects motivation. However, a specific effect on dustbathing motivation cannot be concluded from this finding, since no changes were seen in the subsequent dustbathing behaviour.

### **Sham dustbathing**

Hens have been found to work for access to litter (Matthews *et al.*, 1995; Gunnarsson *et al.*, 2000a), and in conventional battery cages without litter hens sham dustbathe on the wire floor (Vestergaard, 1981a,b). Modified cages are therefore equipped with a dustbath, in order to satisfy hens' motivation for dustbathing. Nevertheless, it has been found that sham dustbathing is frequent among hens in modified cages (Lindberg & Nicol, 1997; Olsson & Keeling, submitted). There are several possible explanations for this sham dustbathing.

It has been suggested that sham dustbathing may in itself be satisfying and hence reduce dustbathing motivation so that it can substitute dustbathing in litter (Lindberg & Nicol, 1997). However, this was not supported by later results, reported by Lindberg (1999) and in paper IV in this thesis, where no effect of sham dustbathing on motivation to dustbathe in litter was found.

Alternatively, sham dustbathing in modified cages could be an effect of the relatively small size of the dustbath, which makes it difficult for more than one hen to dustbathe at a time. This problem would be further aggravated if dustbathing is socially facilitated. However, we have demonstrated that sham dustbathing in modified cages does not seem to be the result of social competition for the limited dustbath space (Olsson & Keeling, submitted) and that there is no effect of social facilitation (paper IV in this thesis).

A third explanation for the sham dustbathing in modified cages may be the effect of early experience, since hens prefer the dustbathing substrate they are used to even in the presence of superior materials (Vestergaard & Lisborg, 1993). This is also supported by the finding of an effect of habit on sham dustbathing in paper IV. Previous research on the effect of rearing conditions on dustbathing behaviour have shown that the motor mechanisms and the organization of dustbathing behaviour develops normally in chicks reared without litter (Vestergaard *et al.*, 1990), but that experience of litter is necessary for the dust recognition mechanism to develop (Hogan, 1994). Birds can learn to dustbathe on abnormal substrates, such as feathers (Vestergaard & Lisborg, 1993) if they have no experience of other dustbathing materials. Similarly, in the absence of a dustbathing substrate, they sham dustbathe (Vestergaard *et al.*, 1990, 1999). In birds reared without litter, sham dustbathing is similar both in organization and amount to the dustbathing in litter in litter-reared birds (Vestergaard, 1990). In the light of this, our results suggest that sham dustbathing in hens reared with litter is a different phenomenon than sham dustbathing in hens reared on wire-floor. The initial reaction in litter-reared hens which are deprived of a dustbathing substrate at a later date, is the complete disappearance of any dustbathing behaviour. Then elements of sham dustbathing appear gradually with increasing deprivation, but only after 23 weeks of deprivation are sham dustbathing sequences as complete as the earlier dustbathing in litter (van Lier & Wiepkema, 1992). When litter-reared hens sham dustbathe, they seem to do so even when there are only weak external stimuli present, as in paper IV when hens dustbathed on the concrete floor which was swept clean daily, far from the most salient dusty stimulus in the pen which was the feeders. Altogether, it seems as if this sham dustbathing is a sign of an extremely high internal motivation to dustbathe. The phenomenon of sham dustbathing in hens reared without litter seems to be rather different, being more similar to the normal dustbathing behaviour of hens reared with litter (Vestergaard *et al.*, 1990). The sham dustbathing seen in hens reared without litter is often seen near the feed trough, where the birds can reach the feed (Lindberg & Nicol, 1997; Olsson & Keeling, submitted). Hogan (1994) suggested that development of the full dustbathing mechanism is dependent on experience for establishing the dust recognition. For birds reared in cages without litter, their only experience will be that of sham dustbathing while bill-raking in the feed. As a consequence, this type of sham dustbathing will be the dustbathing behaviour which these hens develop. Given this fundamental difference in the background of the development of sham dustbathing, it may not be correct to extrapolate results from studies of sham dustbathing in litter-reared hens, as in paper IV in this thesis, to hens reared without litter, as would normally be the case with hens housed in modified cages. There is a need for more research on the effect of rearing conditions on sham dustbathing in modified cages.

## Synthesis and animal welfare implications

The research in this thesis has been carried out against the background of changes in Swedish and European legislation for the housing of laying hens, which now requires that birds should have access to litter, perches and nests. The modified cage is one of the systems which fulfils the requirements and has received renewed attention in the discussion of how to improve hen welfare while retaining profit in egg production. It is difficult to predict what impact the modified cages will have in future egg production in Europe, but it is likely that the modified cages will attract a number of egg producers who are not prepared to make such a drastic change as moving over to loose-housing systems.

The modified cages solve a number of welfare problems associated with battery cages and thus imply a substantial improvement of the birds' living conditions. Nevertheless, some of the results of our research indicate the limitations of the modified cages as well as the need for further research and development. The frequent sham dustbathing on the wire floor in even the most recent versions of the modified cages (Olsson & Keeling, submitted) is one such finding. Although the welfare consequences of this sham dustbathing is not clear, it implies that the birds fail to use the dustbaths as intended. The effect of rearing conditions on dustbathing in modified cages is an aspect which needs to be investigated. Also, the finding of a preference for high perches in paper I points to a possible shortcoming of the modified cages, in which the perches are placed only a few centimetres over the cage floor.

Moreover, although research has focused on perching, dustbathing and nesting as key behaviours for laying hens, these are not the only important behaviours for hens. Time budget studies show that feeding and foraging make up the majority of the active period in hens and that they spend a considerable time scratching and pecking on the ground also when they are provided with high-quality feed *ad libitum* in a food hopper (Dawkins, 1989; Bubier, 1996a). A rebound in the behaviour was found by birds deprived of the opportunity to forage, whereas depriving birds of feed did not increase foraging, suggesting the existence of a foraging motivation independent of hunger (Moffat, 2000). Although hens can scratch and peck in the dustbath in modified cages, the limited space and limited opening hours do not permit all hens to engage in these activities for long periods of time.

I would like to make an additional remark concerning motivation, behaviour and animal welfare. The role of internal and external factors is often mentioned and it is assumed that it is more important for an animal to perform behaviours for which the motivation is largely governed by internal factors (*e. g.* Petherick & Rushen, 1997). However, it is important to remember that external factors which increase motivation may be present without us being aware of them. For example, in paper I in this thesis the hens attempted to perch on the horizontal division

between netting and the solid board making up the pen walls, indicating that a stimulus for perching was still present although the perch had been removed. In the same way, an external stimulus for dustbathing is always present even in cages, in the form of feed particles.

In summary, the results presented in this thesis have several implications for the welfare of laying hens. The importance of perching behaviour is underlined by the findings that hens work for access to a perch and that they take longer to settle when a perch is not available to them at night. That dustbathing motivation is not strongly affected by social facilitation means that it may not be a problem for several hens in a modified cage to share one dustbath. On the other hand, the frequent sham dustbathing in modified cages indicates a problem, which in combination with the finding of an effect of habit on sham dustbathing should lead to considerations about how to rear birds for living in modified cages.

## **Conclusions**

Hens are motivated to perch at night and show a preference for higher perches. An effect of social factors on perching motivation could not be found, but hens perch tightly together.

Although observing dustbathing hens affected behaviour, no effect of social facilitation on dustbathing behaviour could be found. In combination with a reinterpretation of previous research, this suggests that the effect of social facilitation is weak compared to other factors affecting dustbathing motivation.

Sham dustbathing does not reduce motivation to dustbathe in litter in litter-reared hens. Neither is sham dustbathing affected by social facilitation in the presence of birds dustbathing in litter.

Previous experience of sham dustbathing results in some birds showing sham dustbathing even in the presence of litter. In combination with the finding of frequent sham dustbathing in cage-reared birds in modified cages, it is suggested that sham dustbathing can be a consequence of rearing without litter.

## Svensk sammanfattning

Ett växande motstånd mot burhållning av höns har lett till att både svensk och europeisk lagstiftning har förändrats och att alternativa inhysningssystem för värphöns utvecklats. Strävan har varit att utveckla system som tillåter hönorna att utföra viktiga beteenden som att sitta på sittpinne, värpa i rede och ströbada. För att de nya inhysningssystemen ska utgöra den förbättring man eftersträvar är det viktigt att känna till hur hönornas motivation för att utföra dessa beteenden regleras. Av de många faktorer som påverkar motivation är andra individers beteenden en av de viktigaste för grupplevande djur som hönor. Sociala effekter kan vara särskilt viktiga för beteende och motivation hos hönor i modifierade burar där de begränsade resurserna i form av rede och ströbad inte kan utnyttjas av alla hönor samtidigt. Om ett beteende påverkas av sociala facilitering, det vill säga att motivationen ökar hos en höna som ser en annan höna utföra beteendet, blir det begränsade utrymmet ett problem. Syftet med denna studie var att öka kunskapen om hönors motivation att använda sittpinne och att studera hur sociala faktorer påverkar motivationen att ströbada.

Artikel I beskriver en studie av användningen av sittpinne i en grupp hönor. Vidare studerades beteende när sittpinnarna inte var tillgängliga. När hönorna hade tillgång till sittpinnar använde samtliga hönor dessa för nattvila. Alla hönor satt på de högsta sittpinnarna och de satt tätt tillsammans, trots att det var gott om plats. När sittpinnarna inte var tillgängliga visade hönorna tecken på oro, gick mer och tillbringade mindre tid sittande.

Artikel II beskriver en studie där hönornas motivation för att sitta på sittpinne mättes med hjälp av operant teknik. Den metod som användes var en så kallad push-door. Detta är en svängdörr som kan kopplas till en elektromagnet och genom att strömstyrkan varierar kan dörrens motstånd varieras. Genom att placera dörren så att hönan måste passera genom den för att komma till en resurs kan hönans motivation för att få tillgång till olika resurser mätas. I det första experimentet fick hönorna tillgång till en sittpinne på andra sidan dörren. Beteendet i denna situation jämfördes med i en kontrollsituation utan sittpinne. I det andra experimentet studerades hur närvaron av en annan höna påverkade motivationen. Samma uppställning användes, men resurserna var antingen en sittpinne med en annan höna på pinnen eller samma sittpinne med en annan höna på golvet. I det första experimentet öppnade hönorna tyngre dörrar för att komma till sittpinnen än i kontrollsituationen, vilket visar att de var motiverade för att få tillgång till sittpinne för nattvila. I det andra experimentet öppnade bara hälften av hönorna dörren och ingen effekt av behandlingen kunde påvisas. Denna studie är den första där det visats att hönor är motiverade att använda sittpinne.

Artikel III beskriver två experiment där de sociala effekterna på ströbadningsmotivering studerades. Testhönorna kunde se ett stimulus som bestod antingen av ströbadande hönor, hönor på strö som inte ströbadade eller enbart strö. Därefter fick testhönorna själva tillgång till strömaterial. Beteende studerades både under den tid hönorna exponerades för stimuli och när de hade tillgång till strö. Testhönornas ströbadning påverkades inte av stimulushönornas beteende. Detta tyder på att social facilitering inte har stor betydelse för hönors motivation att ströbada.

Artikel IV behandlar tomgångsströbadning, som innebär att hönorna utför ströbadningsrörelserna men utan strö, till exempel på burens nätgolv. I en tidigare studie har det visat sig att detta är vanligt i modifierade burar, trots att det finns ett ströbad i dessa burar. Syftet med de tre experimenten i artikel IV var att närmare undersöka bakgrunden till denna tomgångsströbadning. Före experimentens början hölls hönorna utan strö i upp till 10 veckor för att tomgångsströbadning skulle utvecklas. I det första experimentet placerades hönorna i en situation där de antingen kunde ströbada i strö, tomgångsströbada eller inte ströbada alls. Sedan gavs de tillgång till strö, och deras beteende under testets båda delar registrerades. Möjligheten att ströbada under den första perioden påverkade inte hur mycket hönorna därefter ströbadade i strö, vilket tyder på att tomgångsströbadning inte minskar motivationen att ströbada. I det andra experimentet kunde hönor som inte hade tillgång till strö se ett stimuli bestående av antingen ströbadande hönor på strö, hönor på strö men som inte ströbadade eller hönor som inte hade strö och som inte ströbadade. Vilket stimulus hönorna utsattes för hade ingen betydelse för om de tomgångsströbadade eller inte, vilket visar att social facilitering inte påverkar tomgångsströbadning. I det tredje experimentet fick hönorna, som tidigare hållits utan strö, tillgång till strö på en annan plats än den där de brukade tomgångsströbada. Även om de flesta hönor ströbadade i ströet den första dagen fortsatte vissa hönor att tomgångsströbada under flera dagar trots att strö fanns tillgängligt. Detta tyder på att vana eller tidigare erfarenhet har betydelse för om hönor tomgångsströbadar.

Sammanfattningsvis visar sittpinnestudierna att hönor som är uppfödda med tillgång till sittpinnar är motiverade att använda dessa för nattvila. Studien av ströbadning visar att social facilitering inte är viktigt för motivationen att ströbada. Tomgångsströbadning minskar inte motivationen för att ströbada och kan inte heller förklaras av social facilitering och konkurrens om begränsat utrymme i ströbadet. Icke desto mindre förekommer tomgångsströbadning ofta i modifierade burar med ströbad. En möjlig förklaring till detta är att hönor som fötts upp utan strö och som därför börjat att tomgångsströbada fortsätter att göra så trots att strö finns tillgängligt.

## References

- Abrahamsson, P. 1996. *Furnished cages and aviaries for laying hens*. Dissertation. Swedish University of Agricultural Sciences. Department of Animal Nutrition and Management. Report 234.
- Appleby, M.C. 1993. Should cages for laying hens be banned or modified? *Animal Welfare* 2, 67-80.
- Appleby, M.C. 1995. Perch length in cages for medium hybrid laying hens. *British Poultry Science* 36, 23-31.
- Appleby, M.C. & Duncan, I.J.H. 1989. Development of perching in hens. *Biology of Behaviour* 14, 157-168.
- Appleby, M.C., Smith, S.F. & Hughes, B.O. 1992. Individual perching behaviour of laying hens and its effects in cages. *British Poultry Science* 35, 227-238.
- Appleby, M.C., Smith, S.F. & Hughes, B.O. 1993. Nesting, dust bathing and perching by laying hens in cages: effects of design on behaviour and welfare. *British Poultry Science* 34, 835-847.
- Blokhuys, H.J. 1984. Rest in poultry. *Applied Animal Behaviour Science* 12, 289-303.
- Broom, D.M. 1998. Welfare, stress and the evolution of feelings. *Advances in the Study of Behaviour* 27, 371-403.
- Bubier, N.E. 1996a. The behavioural priorities of laying hens: the effect of cost/no cost multi-choice tests on time budgets. *Behavioural Processes* 37, 225-238.
- Bubier, N.E. 1996b. The behavioural priorities of laying hens: the effect of two methods of environmental enrichment on time budgets. *Behavioural Processes* 37, 239-249.
- Clayton, D.A. 1978. Socially facilitated behaviour. *The Quarterly Review of Biology* 53, 373-392.
- Cooper, J.J. & Appleby, M.C. 1995. Nesting behaviour of hens: Effects of experience on motivation. *Applied Animal Behaviour Science* 42, 283-295.
- Cooper, J.J. & Appleby, M.C. 1996. Demand for nest boxes in laying hens. *Behavioural Processes* 36, 171-182.
- Cooper, J.J. & Appleby, M.C. 1997. Motivational aspects of individual variation in response to nestboxes by laying hens. *Animal Behaviour* 54, 1245-1253.
- Dawkins, M.S. 1983. Battery hens name their price: Consumer demand theory and the measurement of ethological "needs". *Animal Behaviour* 31, 1195-1205.
- Dawkins, M.S. 1988. Behavioural deprivation: a central problem in animal welfare. *Applied Animal Behaviour Science* 20, 200-225.
- Dawkins, M.S. 1989. Time budgets in red junglefowl as a baseline for the assessment of welfare in domestic fowl. *Applied Animal Behaviour Science* 24, 77-80.
- Dawkins, M.S. 1990. From an animal's point of view: Motivation, fitness and animal welfare. *Behavioural and Brain Sciences* 13, 1-61.
- Dawkins, M. S. 1998. Evolution and animal welfare. *The Quarterly Review of Biology* 73, 305-328.
- Dawkins, M.S. & Beardsley, T. 1986. Reinforcing properties of access to litter in hens. *Applied Animal Behaviour Science* 15, 351-64.
- Duncan, E.T., Appleby, M.C. & Hughes, B.O. 1992. Effect of perches in laying cages on welfare and production of hens. *British Poultry Science* 33, 25-35.
- Duncan, I.J.H. 1970. Frustration in the fowl. In: Freeman, B.M. & Gordon, R.F. (eds). *Aspects of poultry behaviour*. British Poultry Science Ltd. Edinburgh. UK. pp 15-30.
- Duncan, I.J.H. & Wood-Gush, D.G.M. 1971. Frustration and aggression in the domestic fowl. *Animal Behaviour* 19, 500-504.
- Duncan, I.J.H. & Wood-Gush, D.G.M. 1972. Thwarting of feeding behaviour in the domestic hen. *Animal Behaviour* 20, 444-451.



- Duncan, I.J.H. & Fraser, D. 1997. Understanding animal welfare. In: Appleby, M.C. & Hughes, B.O. (eds) *Animal Welfare*. CAB International. Oxon, UK. pp 19-31.
- Duncan, I.J.H., Savory, C.J. & Wood-Gush, D.G.M. 1978. Observations on the reproductive behaviour of domestic fowl in the wild. *Applied Animal Ethology* 4, 29-42.
- Duncan, I.J.H., Widowski, T.M., Malleau, A.E., Lindberg, A.C. & Petherick, J.C. 1998. External factors and causation of dustbathing in domestic hens. *Behavioural Processes* 43, 219-228.
- European Union. 1999. Council directive 1999/74/EC. Brussels.
- Faure, J.M. & Lagadic, H. 1994. Elasticity of demand for food and sand in laying hens subjected to variable wind speed. *Applied Animal Behaviour Science* 42, 49-59.
- Follensbee, M.E., Duncan, I.J.H. & Widowski, T.M. 1992. Quantifying nesting motivation of domestic hens. *Journal of Animal Science* 70, Supplement 1.
- Foster, T.M., Temple, W. & Poling, A. 1997. Behavior analysis and farm animal welfare. *The Behavior Analyst* 20, 87-95.
- Fraser, D. & Matthews, L.R. 1997. Preference and motivation testing. In Appleby, M.C. & Hughes, B.O. (eds) *Animal Welfare*. CAB International. pp 159-173.
- Freire, R., Appleby, M.C. & Hughes, B.O. 1997. Assessment of pre-laying motivation in the domestic hen using social interaction. *Animal Behaviour* 54, 313-319.
- Gunnarsson, S., Keeling, L.J. & Svedberg, J. 1999. Effects of rearing factors on the prevalence of floor eggs, cloacal cannibalism and feather pecking in commercial flocks of loose housed laying hens. *British Poultry Science* 40, 12-18.
- Gunnarsson, S., Matthews, L.R., Foster, T.M. & Temple, W. 2000a. The demand for straw and feathers as litter substrates by laying hens. *Applied Animal Behaviour Science* 65, 321-330.
- Gunnarsson, S., Yngvesson, J., Keeling, L.J. & Forkman, B. 2000b. Rearing with early access to perches enhances spatial awareness in the domestic hen. *Applied Animal Behaviour Science* 67, 217-228.
- Hogan, J.A. 1994. Structure and development of behavior systems. *Psychonomic Bulletin and Review* 1, 439-450.
- Hogan, J.A. & Van Boxel, F. 1993. Causal factors controlling dustbathing in Burmese red junglefowl: some results and a model. *Animal Behaviour* 46, 627-635.
- Hughes, B.O. & Duncan, I.J.H. 1988. The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour* 36, 1696-1707.
- Hughes, B.O. & Channing, C.E. 1998. Effect of restricting access to litter trays on their use by caged laying hens. *Applied Animal Behaviour Science* 56, 37-45.
- Jensen, P. & Toates, F.M. 1993. Who needs "behavioural needs"? Motivational aspects of the needs of animals. *Applied Animal Behaviour Science* 37, 161-181.
- Keeling, L.J. 1997. A comparison of two basic characteristics of a perch for laying hens. In: *Proceedings of the 31<sup>st</sup> Congress of the International Society for Applied Ethology*. Prague. Czech Republic.
- Kent, J.P., McElligott, A.G. & Budgey, H.V. 1997. Ground-roosting in domestic fowl (*Gallus gallus domesticus*) in the Gambia: the anticipation of night. *Behavioural Processes* 39, 271-278.
- Lambe, N.R. & Scott, G.B. 1998. Perching behaviour and preferences for different perch designs among laying hens. *Animal Welfare* 7, 189-202.
- Lazarus, J. 1972. Natural selection and the function of flocking in birds: a reply to Murton. *Ibis* 114, 556-558.
- van Liere, D.W. 1992. The significance of fowls' bathing in dust. *Animal Welfare* 1, 187-202.
- van Liere, D.W. & Wiepkema, P.R. 1992. Effects of long-term deprivation of sand on dustbathing behaviour in laying hens. *Animal Behaviour* 43, 549-558.

- Lindberg, A.C. 1999. Effects of vacuum and real dustbathing bouts on dustbathing motivation in domestic hens. In: *Proceedings of the 33<sup>rd</sup> Congress of the International Society for Applied Ethology*. Lillehammer, Norway.
- Lindberg, A.C. & Nicol, C.J. 1997. Dustbathing in modified battery cages: Is sham dustbathing an adequate substitute? *Applied Animal Behaviour Science* 55, 113-128.
- Lundberg A. S. & Keeling L. J., Social facilitation or social inhibition? Rank affects the response to a video of a dustbathing hen (*Gallus gallus domesticus*). Submitted.
- Mason, G., McFarland, D. & Garner, J. 1998. A demanding task: using economic techniques to assess animal priorities. *Animal Behaviour* 55, 1071-1075.
- Matthews, L.R.; Temple, W.; Foster, T.M.; Walker, J. & McAdie, T.M. 1995. Comparison of the demand for dustbathing substrates by layer hens. In: *Proceedings of the 29<sup>th</sup> Congress of the International Society for Applied Ethology*. Exeter, UK.
- Mench, J.A. & Mason, G.J. 1997. Behaviour. In Appleby, M C & Hughes, B O (eds) *Animal Welfare*. CAB International. pp 127-141.
- McBride, G., Parer, I.P. & Foenander, F. 1969. The social organisation and behaviour of the feral domestic fowl. *Animal Behaviour Monographs* 2, 127-181.
- Moffat, L. 2000. An investigation into the importance of foraging behaviour to laying hens. Unpublished Masters thesis. University of Guelph, Canada
- Nicol, C.J. & Guilford, T. 1991. Exploratory activity as a measure of motivation in deprived hens. *Animal Behaviour* 41, 333-341.
- Olsson, I.A.S., Keeling, L.J. & McAdie, T.M. The push-door for measuring motivation in hens: An adaptation and a critical discussion of the method. *Animal Welfare*. Accepted for publication.
- Olsson, I.A.S & Keeling, L. J. Sham dustbathing in modified cages for laying hens: the effect of dustbath design and opening times. Submitted.
- Petherick, J.C & Rushen, J. 1997. Behavioural restriction. In: Appleby, M.C. & Hughes, B.O. (eds) *Animal Welfare*. CAB International. Oxon, UK. pp 89-105.
- Petherick, J.C. & Rutter, S.M. 1990. Quantifying motivation using a computer-controlled push-door. *Applied Animal Behaviour Science* 27, 159-167.
- Petherick, J.C., Seawright, E., Waddington, D., Duncan, I.J.H. & Murphy, L.B. 1995. The role of perception in the causation of dustbathing behaviour in domestic fowl. *Animal Behaviour* 49, 1521-1530.
- Sandøe, P. & Hurnik, F. (eds). 1996. Welfare of domestic animals. Concepts, theories and methods of measurements. *Acta Agriculturae Scandinavica, Section A Animal Science Supplementum* 27. 115 pp
- Vestergaard, K. 1981a. Behavioural and physiological studies of hens on wire floor and in deep litter pens. *Tierhaltung* 12, 115-132.
- Vestergaard, K. 1981b. The well-being of the caged hen – an analysis based on the normal behaviour of fowls. *Tierhaltung* 12, 145-167.
- Vestergaard, K. 1982. Dust-bathing in the domestic fowl – diurnal rhythm and dust deprivation. *Applied Animal Ethology* 8, 487-495.
- Vestergaard, K. & Lisborg, L., 1993. A model of feather pecking development which relates to dustbathing in the fowl. *Behaviour* 126, 89-105.
- Vestergaard, K., Hogan, J.A. & Kruijt, J.P. 1990. The development of a behavior system: Dustbathing in the Burmese Red Junglefowl I. The influence of the rearing environment on the organization of dustbathing. *Behaviour* 112, 99-115.
- Vestergaard, K.S., Damm, B.I., Abbott, U.K. & Blidsøe, M., 1999. Regulation of dustbathing in feathered and featherless domestic chicks: The Lorenzian model revisited. *Animal Behaviour* 58, 1017-1025.
- Webster, A.B. & Hurnik, J. F. 1994. Synchronization of behavior among laying hens in battery cages. *Applied Animal Behaviour Science* 40, 153-165.
- Widowski, T.M. & Duncan I.J.H. 2000. Working for a dustbath: Are hens increasing pleasure rather than relieving suffering? *Applied Animal Behaviour Science* 68, 39-53.

Wood-Gush, D G M, Duncan, I J H & Savory, C J. 1978. Observations on the social behaviour of domestic fowl in the wild. *Biology of Behaviour* 3, 193-205.

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