

Egg production in furnished cages

Doctoral Dissertation

Eija Valkonen



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Egg production in furnished cages

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Abstract

In the European Union, conventional cages for laying hens will be faded out at the beginning of 2012. The rationale behind this is a public concern over animal welfare in egg production. As alternatives to conventional cages, the European Union Council Directive 1999/74/EC allows non-cage systems and enriched (furnished) cages. Layer performance, behavior, and welfare in differently sized furnished cages have been investigated quite widely during recent decades, but nutrition of hens in this production system has received less attention.

This thesis aims to compare production and feed intake of laying hens in furnished and conventional cages and to study the effects of different dietary treatments in these production systems, thus contributing to the general knowledge of furnished cages as an egg production system. A furnished cage model for 8 hens was compared with a 3-hen conventional cage.

Three consecutive experiments each studied one aspect of layer diet: The first experiment investigated the effects of dietary protein/energy ratio, the second dietary energy levels, and the third the effects of extra limestone supplementation. In addition, a fourth experiment evaluated the effects of perches on feed consumption and behavior of hens in furnished cages.

The dietary treatments in experiments 1–3 generally had similar effects in the two cage types. Thus, there was no evidence supporting a change in nutrient requirements for laying hens when conventional

cages are replaced with small-group furnished cages. Moreover, the results from nutritional experiments conducted in conventional cages can be applied to small-group furnished cage systems.

These results support the view that production performance comparable with conventional cages can be achieved in furnished cages. All of the advantages of cages for bird welfare are sustained in the small-group furnished cages used here. In addition, frequent use of perches and nests implies a wider behavioral repertoire in furnished cages than in conventional cages. The increase observed in bone ash content may improve bird welfare in furnished cages.

The presence of perches diminished feed consumption during the prelaying period and enhanced the feed conversion ratio during the early laying period in furnished cages. However, as the presence or absence of perches in furnished cages had no significant effect on feed consumption after the prelaying period, the lower feed consumption observed in furnished cages than in conventional cages could be attributed to other factors, such as the presence of wood shavings or a nest box. The wider feed trough space per hen in conventional than in furnished cages may partly explain the higher feed consumption observed in conventional cages.

Keywords:

laying hen, furnished cage, enriched cage, egg production, nutrition, behavior

Munivien kanojen varustellut häkit

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Tiivistelmä

Euroopan unionin neuvoston antama direktiivi (1999/74/EY) määrittää munantuotantoon käytettävien kanojen suojelua koskevat vähimmäismääräykset. Direktiivi kieltää perinteisten varustelemattomien häkkien käytön munivien kanojen pitopaikkana vuoden 2012 alusta. Munantuotanto on tämän jälkeen mahdollista joko niin kutsutuissa vaihtoehtoisissa järjestelmissä, joita ovat lattia- ja kerroslattiakanalat, tai varustelluissa ns. virikehäkeissä. Muutoksia perustellaan eläinten hyvinvoinnin parantumisella.

Varustelluissa häkeissä on kanaa kohti enemmän tilaa kuin perinteisissä varustelemattomissa häkeissä. Lisäksi varustelluissa häkeissä kanojen käytettävissä on orret, munintapesä ja pehkualue. Varusteltuja häkkeitä on kehitetty jo vuosikymmenten ajan, mutta kanojen ruokintaa ja ravinnontarvetta tässä tuotantomuodossa on tutkittu vain vähän. Tämän tutkimuksen tarkoituksena oli verrata varusteltuja ja perinteisiä häkkeitä munantuotantomenetelmänä, selvittää varustelluissa häkeissä pidettävien kanojen ravintoaineiden tarvetta sekä kanojen orren, munintapesän ja pehkualueen käyttöä varustelluissa häkeissä.

Kolmessa koko munintakauden kestävässä tutkimuksessa selvitettiin kussakin yhden rehutekijän vaikutusta kanojen tuotantoon

ja kuntoon kolmen kanan perinteisissä ja kahdeksan kanan varustelluissa häkeissä. Tutkittavat tekijät olivat rehun valkuaispitoisuus, energiasisältö ja kalsiumlisä. Varustelluissa häkeissä seurattiin kanojen orsien, pesän ja pehkualueen käyttöä. Neljännessä tutkimuksessa selvitettiin orren vaikutusta kanojen rehunkulutukseen ja käyttäytymiseen varustelluissa häkeissä.

Koska tutkittujen rehujen vaikutukset olivat samansuuntaiset ja -suuruiset perinteisissä ja varustelluissa häkeissä, voidaan todeta, että kanojen nykyiset ruokintasuosituksukset pätevät myös varustelluissa häkeissä. Tulosten perusteella varustelluissa häkeissä voidaan saavuttaa perinteisten häkkien tuotantotasoa. Tuotannon kannattavuuden kannalta tärkeä rehunmuutosuhde eli rehunkulutus tuotettua munakiloa kohden oli tutkituissa häkkityypeissä sama. Orsien ja munintapesän runsas käyttö kertoo kanojen pystyvän toteuttamaan tiettyjä lajinmukaisia käyttäytymismalleja varustelluissa häkeissä. Varustelluissa häkeissä havaittu parempi luuston mineralisoituminen tukee myös oletusta kanojen parantuneesta hyvinvoinnista.

Avainsanat:

kana, varusteltu häkki, virikehäkki, munantuotanto, ruokinta, käyttäytyminen

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List of original publications

This thesis is based on the following publications:

- I Valkonen, E., Venäläinen, E., Rossow, L., and Valaja, J. 2006. Effects of dietary protein on egg production of laying hens housed in furnished or conventional cages. *Acta Agriculturae Scandinavica, Section A. Animal Science* 56:33–41.
- II Valkonen, E., Venäläinen, E., Rossow, L., and Valaja, J. 2008. Effects of dietary energy content on the performance of laying hens in furnished and conventional cages. *Poultry Science* 87:844–852.
- III Valkonen, E., Venäläinen, E., Rossow, L., and Valaja, J. 2010. Effects of calcium diet supplements on egg strength in conventional and furnished cages, and effects of 2 different nest floor materials. Manuscript accepted for publication in *Poultry Science* August 15, 2010.
- IV Valkonen, E., Rinne, R., and Valaja, J. 2009. Effects of perch on feed consumption and behaviour of caged laying hens. *Agricultural and Food Science* 18:257–267.

These publications are referred to in the text by their Roman numerals.

The articles are reprinted with the kind permission of their respective copyright holders. In addition, some unpublished material is presented.

First author's contribution in publications:

Eija Valkonen participated in practical management and data collection, calculated and interpreted the results, and was responsible for preparation of the paper in study I. In studies II–IV, she planned the experiments with coauthors, participated in practical management and data collection, calculated and interpreted the results, and was responsible for preparation of the papers.

Abbreviations

AME	Apparent metabolizable energy
CC	Conventional cage
EMC	Edinburgh Modified Cage
FC	Furnished cage (also referred to as enriched cage)
FCR	Feed conversion ratio (kg feed/kg eggs)
FLHS	Fatty liver hemorrhagic syndrome
HL diet	High limestone-supplemented diet
IGF-I	Insulin-like growth factor I
ME	Metabolizable energy
NL diet	Normal limestone-supplemented diet
TSAA	Total sulfur amino acids (methionine and cysteine)

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1 Introduction

In the European Union, conventional (or battery) cages for laying hens will be faded out at the beginning of 2012. This change in hens' housing systems is probably one of the biggest challenges the egg-producing industry will meet in our time. The rationale behind this change is a public concern over animal welfare in egg production. As alternatives to conventional cages, the European Union Council Directive 1999/74/EC (Commission of the European Communities 1999) allows non-cage systems and enriched (furnished) cages. According to this directive, an enriched cage must contain a nest, a 15-cm perch for each hen, and litter for pecking and scratching. Such cages must have a total area of at least 2000 cm², offering each hen an area of 750 cm².

1.1 Egg production systems in Europe

In some European countries, a ban of conventional – or all – cages has been already put into action. Switzerland was the first European country to implement a total ban of cages 25 years ago. In Sweden, a ban of conventional cages was enforced in 1997, before other EU countries. All conventional cages have now been phased out in Sweden, and less than 40% of laying hens live in furnished cages, while most of the hens in Sweden live in non-cage systems. In Austria, a ban of all cages was put into effect from the beginning of 2009. However, those farmers who have earlier invested in furnished cages, are allowed to continue egg production in furnished cages until 2020. Over 70% of laying hens in Austria live in non-cage systems. In the Netherlands, the government has decided to ban furnished cages, but will allow “Kleingruppenhaltung”, which is also permitted in Germany instead of furnished cages. Kleingruppenhaltung refers to a large fur-

nished cage, with modified requirements compared with the enriched cage described in the European Union Council Directive 1999/74/EC (Commission of the European Communities 1999), e.g. larger minimum total area (25 000 cm²) and more floor (800 or 900 cm² for light and medium hybrids, respectively), nest (90 cm²), and litter (90 cm²) area per hen.

1.2 Future outlook of production systems in Finland

In Finland, at the end of 2009, the majority of the 3.3 million laying hens were still kept in conventional cages. However, based on a survey (Lastikka 2008, Suomen Gallup Elintarviketieto Oy 2008), about 40% of the producers are predicted to cease production before or at the beginning of 2012. These farms represented 17% of the egg production in 2008. Most of the closing farms have conventional cages (84%), and they are smaller than the farms intending to continue in 2012. The most common reasons for giving up egg production are poor profitability of production (30%) and the cage ban (26%). According to the survey, most of the producers with conventional cages who intend to continue egg production plan to invest in furnished cages (47%). However, one-third of these producers (17% of all producers planning to continue in 2012) have reported conventional cages as their production system in 2012. Finnish authorities are, however, determined to enforce the cage ban from January 2012. In 2012, according to the survey, 48% of hens will be housed in furnished cages, 19% in multi-tier systems, 11% in barns, and 4% of hens will be in organic production. What will happen to the 17% still forecasted to be in conventional cages remains to be seen.

1.3 Cages – pros and cons

In developed countries, barn and free-range systems were commonly replaced with cages between the 1950s and the 1970s (Appleby 2003). There were several reasons for this change. The most prevailing motives were probably economic, but some of the cages' advantages benefit both producer and hen. Production in cages proved to be more profitable due to increased unit size and stocking density, automation, and less labor required, but also because of better health and lower mortality of birds. Better hygiene in cages results in fewer disease outbreaks, and endoparasites are practically absent in cages (Fossum et al. 2009, Savory 2004). Cannibalism tends to be less frequent in cages, and when it does occur it involves fewer birds than in non-cage systems (e.g. Appleby 2003, Rodenburg et al. 2008, Fossum et al. 2009). Group size is probably one factor in this, as mortality due to cannibalism is reported to be higher in systems with large group sizes (Shimmura et al. 2010). Egg eating is mostly prevented in cages, and there are no "floor eggs" in cages to be collected manually. Effective manure removal systems and absence of litter in cages enhances air quality, resulting in lower air dust and ammonia levels (Rodenburg et al. 2008, Nimmermark et al. 2009). Overall, cages give the producer more control over the hens and the production process (Savory 2004).

However, many welfare problems exist in conventional cages for laying hens. Restricted behavior and a barren environment are often identified as the most important threats to hen welfare (Appleby 2003, Savory 2004). Lack of exercise exposes hens to disuse osteoporosis, lack of nesting facilities leads to frustrated prelaying behavior, and deprivation of other dust-bathing substrates manifests itself as sham dust-bathing on a wire mesh floor with feed. In cage confinement, hens are incapable of evading antagonistic cage mates (Savo-

ry 2004). The development of furnished cages has tried to overcome these defects, while simultaneously retaining the advantages of cages.

1.4 Development of furnished cages

Domestic fowl is a descendant of jungle fowl and tends to exhibit behavior similar to its ancestor (e.g. Duncan 1998). Behaviors that have become fixed in evolution have had survival value and have remained unaltered during domestication and artificial selection. In evolution, the actual causation of behavior is often separated from the original function of the behavior. For example, nesting behavior is mainly caused by hormonal and neural stimuli, while its function is to increase the chances of successful hatching of eggs (Duncan 1998). Even when the function of behavior is fulfilled artificially, the behavior may still be stimulated or caused (Duncan 1998). Often, behavior can be separated into two elements: an appetitive phase and a consummatory phase (Hughes and Duncan 1988). For instance, foraging and feed searching are appetitive, while eating is consummatory. Motivation to perform appetitive behavior may not be decreased even when the consummatory behavior is satisfied (Hughes and Duncan 1988). Behavioral needs or priorities have been assessed by studying the motivational strength of hens to engage in various behaviors using consumer demand techniques (e.g. Cooper and Appleby 2003, Olsson et al. 2002).

Nest searching (Freire et al. 1997) and nest building (Cooper and Appleby 2003) have both been identified as behavioral priorities. Hens are also highly motivated to perch, especially at night (Olsson and Keeling 2000, Olsson and Keeling 2002). Hens can use litter for pecking and scratching. Allowing these activities may be important to satisfy the motivation to forage. Hens with access to litter perform less feather pecking than birds without lit-

ter (Nicol et al. 2001). Litter also serves as a dustbathing substrate. Hens are motivated to dustbathe and are willing to work to gain access to litter (Widowski and Duncan 2000, de Jong et al. 2005). Olsson et al. (2002) found no evidence that sham dustbathing would reduce the motivation to dustbathe in litter, and Colson et al. (2007) reported a higher motivation to dustbathe in litter in caged hens without access to litter than in birds housed in aviaries with litter. Thus, sham dustbathing may not be an adequate substitute for dustbathing in litter.

To overcome the restrictions of behavior in cages, furnished cages were developed. Early designs of cages furnished with perches, nest, and litter bath were so-called Get-Away-Cages (Bareham 1976, Elson 1976, Wegner 1990) for groups of 15–25 hens, and the smaller Edinburgh Modified Cage (EMC) for groups of 4 or 5 hens (e.g. Appleby and Hughes 1995). A small-group furnished cage was preferred by some researchers because it proved to be more stable regarding production and mortality, produced better egg quality, offered better inspection possibilities, and was easier to depopulate (e.g. Abrahamsson et al. 1995). However, to diminish investment costs per bird, a bigger group size is beneficial, and therefore, groups of up to 8 hens were studied in a cage design based on EMC (Abrahamsson and Tauson 1997). After successful experiments, the first commercially applied furnished cages housed 8 hens. Group sizes have subsequently been increased to up to 60 birds (e.g. Vits et al. 2005). Increasing group size in furnished cages is associated with poorer plumage (Appleby et al. 2002, Hetland et al. 2003b, Weitzenbürger et al. 2006), higher mortality (Weitzenbürger et al. 2005), and higher feed consumption (Vits et al. 2005). Beak trimming can alleviate these problems, and it is used in most European countries. However, beak trimming itself can be seen as a welfare issue, and thus, it is prohibited in Finland,

Norway, and Sweden. To obviate welfare problems, group size in furnished cages is restricted to 16 birds in Sweden and to 10 birds in Denmark.

Along with group size, nest and dustbaths have evolved. To prevent dustbathing in the nest, laying in the litter box, and soiling of these facilities, automatic doors were introduced (Smith et al. 1993). Later on, the restriction of nest use was widely abandoned, while restricted access to litter is still considered necessary in cages with a separate litter box from which eggs will not roll out to the egg cradle. Another practical problem with this type of dustbaths is that automation of adding the dustbathing substrate is difficult. Other designs of litter area have been introduced, the latest of these being an artificial turf mat placed on the cage floor (e.g. Weitzenbürger et al. 2005). In this design, eggs laid in the litter area will roll out, and thus, are not a problem as such. However, eggs laid on the litter area may be at higher risk of getting dirty.

1.5 Studies on furnished cages

Layer performance, behavior, and welfare in differently sized furnished cages have been studied quite widely in recent decades. Production, feed conversion, and mortality results comparable with conventional cages are reported in furnished cages (Abrahamsson et al. 1995, Abrahamsson and Tauson 1997, Appleby et al. 2002, Guesdon and Faure 2004). Often a bigger proportion of cracked eggs or dirty eggs or both has been reported in furnished than in conventional cages (Abrahamsson et al. 1995, Appleby et al. 2002, Guesdon and Faure 2004, Guesdon et al. 2006, Tactacan et al. 2009). In furnished cages, most eggs are laid in the nest, and thus, they accumulate in a narrower part of the egg cradle than in conventional cages. This increases the risk of collisions between eggs, and consequently, the incidence of cracks.

On the other hand, Guesdon et al. (2006) reported that eggs laid in the other parts of the cage were at greater risk of being broken than eggs laid in nests. In addition, some authors have attributed the greater risk of cracked eggs to perches (Appleby et al. 2002). Possible explanations for greater incidence of dirty eggs are laying in the dustbathing area (Appleby et al. 2002, Tactacan et al. 2009) and nest linings becoming soiled, especially if nests are used widely for purposes other than laying (Vits et al. 2005).

Perches and nest are used extensively in furnished cages (Appleby and Hughes 1995, Abrahamsson et al. 1996, Abrahamsson and Tauson 1997). The litter bath is, however, used rather infrequently and sham dustbathing is common even in furnished cages in the presence of litter (Abrahamsson et al. 1996, Lindberg and Nicol 1997, Olsson and Keeling 2002). Several reasons for the restricted use of the dustbath have been suggested: litter in the dustbath may be quickly depleted, dustbaths may be empty most of the time (Lindberg and Nicol 1997), and competition may occur for the limited dustbathing area (Abrahamsson et al. 1996, Shimmura et al. 2007a). Ease of access and earlier experience may also be of importance for the use of the litter area (Olsson and Keeling 2002, Olsson et al. 2002). Conflicting results have been published on plumage cover in studies comparing furnished and conventional cages (Abrahamsson and Tauson 1997, Hetland et al. 2004). Pododermatitis (bumble foot) and keel bone deformations have been related to the presence of a perch (Appleby et al. 1993, Tauson and Abrahamsson 1994, Abrahamsson et al. 1996). The shape and material of the perch have an impact on both pododermatitis and keel bone lesion incidences, and some research has been done to identify the optimal perch design (Abrahamsson 1996).

Nutrition of hens in furnished cages has received less attention in the literature.

Only a limited number of reports include replicated measurement of feed consumption in furnished cages in comparison with conventional cages (Appleby et al. 2002; Hetland et al. 2003b, 2004; Shimmura et al. 2007b, 2007c, 2009, 2010), and nutritional treatments in these reports are even scarcer (Hetland et al. 2003b, 2004). Lower feed intake has been noted in hens housed in cages with perches (Tauson and Jansson 1988, Braastad 1990, Glatz and Barnett 1996). This was hypothesized to be a result of less locomotor activity observed in birds with access to perches (Braastad 1990) and clogging of birds on the perch, leading to less heat losses (Tauson and Jansson 1988). Provision of perches and litter material may diminish feather damage (Braastad 1990, Abrahamsson and Tauson 1997), and feather cover affects a bird's energy requirements and feed intake (Tauson and Svensson 1980, Peguri and Coon 1993). Birds are known to ingest litter, and this may lead to higher satiety, as coarse particles need to be ground in the gizzard before they move on to the small intestine (Hetland et al. 2003b). Birds with access to wood shavings have higher empty gizzard weight and weight of gizzard contents than birds without access to litter (Hetland et al. 2003a, Hetland and Svihus 2007). A well-functioning gizzard enhances nutrient digestibility (Hetland and Svihus 2007). These results suggest that hens in furnished cages may consume less feed than hens in conventional cages. Conflicting results have, however, been reported in studies comparing conventional and furnished cages (e.g. Hetland et al. 2003b, 2004). In practice, switching egg production from conventional to furnished cages will result in larger group sizes. Increased group size and bird density in cages lead to lower egg production and feed use (Adams and Craig 1985, Sohail et al. 2001, 2004). However, in experiments with constant space allowance and feeder space per hen, Carey et al. (1995) and Abrahamsson and Tauson (1997) reported no effects of increased group size on hen performance.

Increased group size may negatively affect plumage condition (Appleby et al. 2002, Hetland et al. 2003b, Weitzenbürger et al. 2006). When increased group size is associated with increased total area, bird activity tends to increase (Carey et al. 1995). Group size may therefore be one of the factors affecting the results in studies comparing conventional and furnished cages.

1.6 Feed intake and feed formulation

Feed costs typically comprise a major part of the total costs of commercial egg production. Thus, the efficient use of feeds and feed stuffs is essential for the profitability of egg production.

To be able to formulate a diet that offers a specific daily nutrient intake, a prediction of daily feed intake is needed (Gous 1986). Knowledge of factors that affect feed intake is also critical in diet formulation. Feed intake is affected by multiple factors, such as the bird's live weight, egg production, activity, plumage cover, ambient temperature, and feed characteristics (McDonald 1978, Tauson and Svensson 1980, Rose 1997).

Generally, hens adjust their feed intake according to their energy requirements and dietary energy (McDonald 1978). If a change in production system has an effect on feed intake, the change in daily nutrient intake can be corrected by a change in feed nutrient content. However, if similar daily nutrient intakes produce different production

responses or efficiencies in different production systems, a change in nutrient requirements is assumed (NRC 1981).

1.7 Aims of the thesis

The main aim of this thesis was to study a small-group furnished cage as an egg production system. The effects of this system on laying hens' nutrition, feeding, and production, as well as on health and external conditions were investigated using the results from conventional cages as a point of comparison. In addition, the behavior of hens was evaluated in furnished cages, and three different perch designs and two different nest floorings were compared.

Differences in feed intake between the two production systems may reflect differences in energy requirements and may warrant different dietary specifications. The first three experiments each examined one important element of layer hen nutrition: protein, energy, and calcium, and their effects on hen production and health.

In studies comparing conventional 3-hen cages and 8-hen furnished cages, the effects of group size and space allowance intermingle with the effects of the housing system. The fourth experiment investigated the effects of perches without the confounding effects of group size and space allowance to shed light on the possible energy-saving capacity of the perch.

2 Materials and methods

2.1 Experimental design

In the first three experiments (Studies I–III), responses to different diets by laying hens was investigated in either 3-hen conventional cages (CC) or in 8-hen furnished cages (FC) (Figure 1) during 52-week laying periods. In each of these experiments, two dietary treatments were randomly allocated to two housing systems (CC and FC). Both housing systems formed a cage bank and they located in the same environmentally controlled windowless room, side by side. Housing systems could not be randomized over these two banks, and despite this, an assumption of independent observations was made.

The first two experiments (Studies I–II) had 16 replicates per treatment and had a $2 \times$

2 factorial design (2 dietary treatments \times 2 housing systems). In addition, the first two experiments investigated the effects of three different perch designs on birds' foot-pad condition and perching behavior in FC. Two wooden designs (one with a round and the other with an angular cross-section) and one plastic perch design (T-shaped cross-section) were used (Figure 2). In the third experiment (Study III), 16 replicates per diet in CC and 20 replicates per diet in FC were applied. The third experiment (Study III) had a third factor within FC, as two different nest floor materials, an artificial turf and a smooth perforated plastic, were compared (Figure 3). These different nest floorings were randomly assigned to 20 replicates each. This yields 10 replicates per diet \times floor treatments in FC.



Fig. 1. Furnished cage for eight hens.

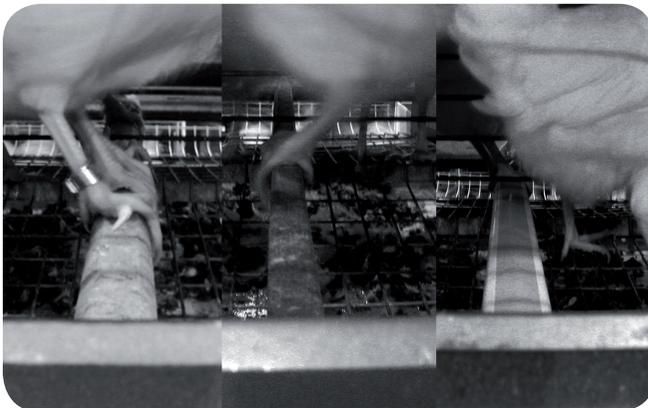


Fig. 2. The three different perch designs used in Experiments 1 and 2. From left: wooden perch with round cross-section, wooden perch with angular cross-section, and plastic perch with T-shaped cross-section.

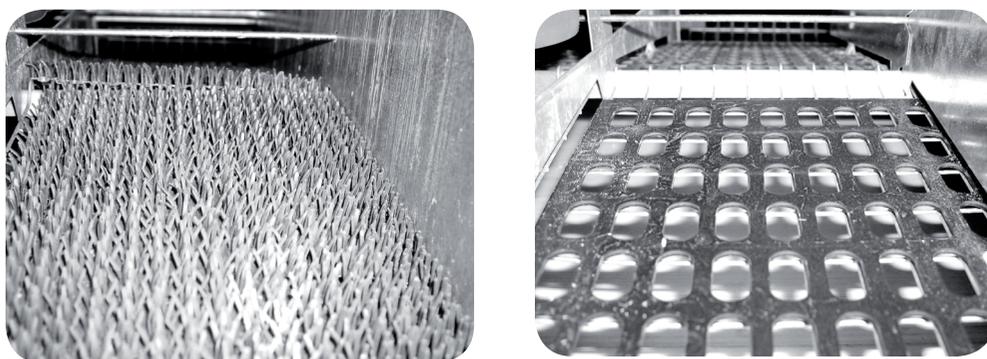


Fig. 3. The two different nest floor materials used in Experiment 3. Left: Artificial turf. Right: Smooth perforated plastic.

The fourth experiment (Study IV) evaluated the effects of perches in FC. The experiment started at housing at 16 weeks of age and lasted for 29 weeks. The control treatment (P16) hens were housed in cages furnished completely in accordance with Council Directive 1999/74/EC (Commission of the European Communities 1999). In the other two treatments, perches were removed from the cages before housing the pullets. No-perch (NP) cages remained without perches throughout the experiment, and perches were installed in P19 cages at 19 weeks of age. These three different treatments were randomly allocated to 22 replicates (6, 6, and 10 replicates per treatments P16, P19, and NP, respectively).

2.2 Animals, housing, and management

All of the experiments used the same commercial strain of white single comb Leghorn chicken (Lohmann Selected Leghorn, LSL Classic). In Experiments 1, 2, and 4, the pullets were 16 weeks, and in the Experiment 3 the pullets were 17 weeks of age at the time of housing. A commercial rearing farm reared the birds in conventional cages. During the first week following housing, birds in Experiments 1–2 received 8.5 h and birds in experiment 3 received 9 h of light per day. The photoperiod was gradually increased to 14.5 h of

light per day at 25 weeks of age. The birds in Experiment 4 received 10 h of light per day during the first week following housing, and, after this, the photoperiod was increased to 14.5 h at 17 weeks of age. The first 2 lines of the 4 light lines used went on and off about 3 min before the rest of the lines to imitate dawn and dusk.

Feeds were distributed to each experimental unit (replicate) once a week to a hopper container. A chain feeder ran once a day to provide birds their feed. To ensure ad libitum access to feed, about twice the amount of expected daily feed consumption was provided, and the feed trough was never empty. Leftover feed was collected separately for each replicate and reused for the same replicate. Water was available ad libitum from nipple drinker lines.

The design of the furnished cages was based on the Edinburgh Modified Cage concept (Appleby and Hughes 1995), with a nest occupying one end of the cage, and a litter area on top of the nest. The furnished cages (TAPE, Triotec Oy, Koski TL, Finland) measured 120 cm × 50 cm × 48 cm (width × depth × height) and housed 8 hens each, providing 600 cm² of usable area and 750 cm² of total cage area per hen (Figure 1). The length of the feed trough per hen was about 12 cm. In each FC, 3 perches ran through the cage perpendic-

ularly to the feed trough so that the hens were not forced to stand on a perch while feeding. A plastic strip curtain separated the nest from the main cage area, and artificial turf (in Experiments 1–3) or smooth perforated plastic sheet (in Experiments 3 and 4) lined the nest floor. No egg saver device was in use. Perforated egg baffles served as a claw shortener device. Litter box gates opened automatically to let hens into the litter area daily. In the first experiment (Study I), litter boxes were kept closed until the beginning of the experiment at 21 weeks of age, and, after that, they were opened daily for 3 h. In experiments 2–4, litter boxes were available 5 h daily starting from the time of housing. Litter material (wood shavings) was topped up by hand twice a week.

Each conventional cage housed 3 hens and measured 48 cm × 41 cm × 57 cm (width × depth × height), offering about 660 cm² of cage area and 16 cm of feeder space per hen. For claw shorteners, strips of abrasive tape were stuck to egg baffles.

2.3 Diets

During rearing birds were fed commercial rearing diets. After housing at 16–17 weeks of age, pullets received either a

mix of commercial feed concentrate, barley, oats, and limestone (Studies II and III) or a feed comprising barley, soybean meal, wheat, oats, rapeseed oil, minerals, and vitamin and trace element premixes (Studies I and IV). All prelaying diets were pelleted. From 21 weeks of age, layer diets were introduced. In Experiment 4, hens received the same diet through the 24-week laying period. In Experiments 1–3, layer diets were the experimental diets. The effects of the two diets were examined in Experiments 1–3 (Studies I–III). Each dietary treatment comprised three feeds fed over three consecutive feeding phases (Table 1). Feed protein and energy content decreased, and calcium content increased in stages from one phase to the next. All layer diets were pelleted.

Experiment 1 studied the effects of dietary protein to energy ratio. Protein is typically the most expensive component in feed, thus limiting dietary protein content may be economically desirable. In addition, concern about ammonia emission from poultry production has brought about efforts to decrease nitrogen excretion and increase the efficiency of protein utilization in poultry (e.g. Roberts et al. 2007, Veens et al. 2009). Nitrogen excretion of the laying hen can be reduced by feeding lower crude protein diets (Summers 1993, Rob-

Table 1. Description of planned dietary treatments and feeding phases in Experiments 1–3.

		Experiment						
		1		2		3		
	Age (weeks)	Energy (MJ/kg)	Protein (g/kg)	Energy (MJ/kg)	Protein (g/kg)	Energy (MJ/kg)	Protein (g/kg)	Calcium (g/kg)
Phase I	21–41	10.6	173	10.1	148	10.5	156	43.8
	21		131	11.0	163		157	37.3
Phase II	41–57	10.5	171	10.0	147	10.4	156	48.5
	41		129	11.0	162		155	38.0
Phase III	57–73	10.3	171	9.8	144	10.3	155	50.3
	57		131	10.8	160		155	40.2

erts et al. 2007). In Experiment 1, the low-protein diet had about 24% lower crude protein content than the high-protein diet.

Experiment 2 studied the effects of dietary energy using diets formulated to contain equal amounts of other nutrients per kilocalorie of ME. Such diets aim at equal daily nutrient intake in relation to dietary energy. The results of studies of the effects of dietary energy on the laying rate are conflicting. Çiftci et al. (2003), for instance, found that decreasing the energy content of feed from 2751 to 2641 kcal of ME/kg increased the laying rate from 86.44% to 88.27%. However, Mathlouthi et al. (2002) reported increased laying rates at an energy content of 2753 kcal of ME/kg of feed compared with 2653 kcal of ME/kg of feed. In Experiment 2, the dietary energy contents studied were lower, being from 2581 to 2629 kcal/kg of feed in the high-energy diet and from 2342 to 2414 kcal/kg of feed in the low-energy diet.

Laying hens excrete about 2 g of calcium in an eggshell (Gilbert, 1983). If absorption of calcium from the gastrointestinal tract is insufficient at the time of shell formation, resorption from bones supplies calcium for shell formation. Dietary calcium may thus affect egg shell quality and bone mineralization. The dietary level of calcium affects the feed and energy intake of hens, as, for example, Härtel (1989) and Roland and Bryant (1994) demonstrated. Interactions may exist between the effects of dietary calcium level and the effects of production system on feed intake of laying hens. In Experiment 3, experimental diets with two different limestone supplementation levels were compared. Normal limestone supplementation level in the diet was based on the calcium levels currently used in commercial layer feeds in Finland (37–40 g calcium/kg of feed), and it was compared with a diet with an elevated limestone content (44–50 g calcium/kg of feed).

2.4 Data collection

Feed and feed ingredient samples were taken from each feed batch made. The samples were pooled to one sample per feed, and dried and ground for analysis. Feed samples were analyzed for crude protein, crude fat, crude fiber and ash, as well as for amino acid and calcium and phosphorus contents.

Feed refusals were weighed at the end of each 4-week test period, and feed consumption was calculated as the difference between the delivered and refused feed. Eggs were collected daily, separately for each replicate. The number and weight of the eggs were recorded. In FC, also the position of the eggs was recorded. Mean production, feed consumption, and feed conversion ratio (FCR; kg feed per kg eggs) were calculated for each test period. Mortality was recorded daily and cumulative mortality was calculated over the entire experiment. The dead birds were sent to the Finnish Food Safety Authority for autopsies in Experiments 1–3. The hens were weighed at the beginning of the experiments and at the end of each feeding phase.

Egg quality was assessed in a sample of eggs 3 times (at 36, 54, and 68 weeks of age) during Experiments 1–3. Each time, the egg weight, albumen height, specific gravity, and shell strength were measured. Albumen height was converted to Haugh units. In Experiments 1 and 2, also the weights and proportions of albumen, yolk, and shell in a sample of eggs were measured 3 times.

Hens' exterior appearance was scored in all experiments. These results are not presented in Studies I–III, but are presented in Sections 3.3.3 and 3.4.3. In the first 3 experiments, scoring was done 3 times (at 32, 55, and 71 weeks of age) for half of the hens in each replicate. In Experiment 4, scoring was done twice (at 27 and 43

weeks of age). Scorings involved weighing, plumage condition scoring of neck, breast, back, wings, tail, and cloaca, condition scoring of foot pad (pododermatitis), and scoring of keel bone deformation. A scale from 1 (poorest) to 4 (best) was used (Tauson et al. 1984). Plumage scores of the 6 body parts sum up to a total plumage score, ranging from 6 to 24 points, and foot pad score is the mean of the scores of a hen's feet.

Breaking strength of tibia was measured at the end of the experiments in studies 1–3. In addition, tibia ash was measured in Experiments 2 and 3. These data are not presented in Studies I–II, but are included in Sections 3.3.3.3 and 3.4.3.3.

The proportion of hens on the perches and in the nests was recorded on 3 consecutive days three times a day (at 6 and 11.5 h after lights-on, and at 1 h after lights-out) at various ages during the experiments. In Experiments 1–3, these observations were made at 8-week intervals starting in the first week of Period 2. In Experiment 4, observations of hen location were made at 17, 20, 26, 34, and 42 weeks of age. On the same days, the number of hens in the litter boxes was recorded at separate times (at 30 min and at 2 h after the opening of the litter box in Experiments 1–3, and at the time of opening of the litter box and at 30 min and at 2 h after the opening of the litter box in Experiment 4). These data are not presented in Studies I–III, but are included in Section 3.5.1.

The behavior of 9 individual hens (3 hens per treatment) was recorded in Experiment 4 using direct observations and instantaneous sampling at 5-min intervals. Three randomly selected hens per treatment from separate cages were marked with animal marking paint at least 1 day before the observations. The observer sat on a stool in the aisle and recorded the behavior of the 3 marked hens (1 per treatment) simultaneously.

2.5 Calculations and statistical analysis

A row of 6 CC or a pair of FC comprised an experimental unit (replicate). In all experiments, the production variables were subjected to repeated measures of variance. The analyses were performed using the GLM procedure of SAS (SAS Institute Inc., Cary, NC, USA). The GLM procedure computes type III sum of squares, which corrects for unequal replication. The following model was used in Experiments 1 and 2: $Y_{ijk} = \mu + t_i + \delta_i + p_k + (p \times t)_{ik} + \epsilon_{ijk}$, where Y_{ijk} = observation, μ = general mean, t_i = effect of treatment ($i = 1, \dots, 8$), δ_i = error term for effect of treatment, p_k = effect of period ($k = 1, \dots, 13$), and ϵ_{ijk} = experimental error. Other variables were evaluated by analysis of variance using the following model: $Y_{ij} = \mu + t_i + \epsilon_{ij}$, where Y_{ij} = observation, μ = general mean, t_i = effect of treatment ($i = 1, \dots, 6$), and ϵ_{ij} = experimental error. In Experiments 1 and 2, the treatment effects were separated into 7 orthogonal contrasts involving housing system, diet, and the interaction between the effects of housing system and diet, wooden perches vs. plastic perches, round wooden perches vs. angular wooden perches, and the interaction between the effects of diet and the effects of wooden perches vs. plastic perches, and the interaction between the effects of diet and the effects of round wooden perches vs. angular wooden perches. When no significant differences between the effects of perch designs were found, they were omitted from the model and the treatment effects were separated into 3 orthogonal contrasts involving housing system, diet, and the interaction between the effects of housing system and the effects of diet. In Experiment 3, production variables and egg quality variables were evaluated by repeated measures analysis of variance using the following model: $Y_{ijklmn} = \mu + d_i + h_j + n_{k(j)} + (d \times h)_{ij} + (d \times n)_{ik(j)} + \delta_{(ijk)l} + p_m + (d \times p)_{im} + (h \times p)_{jm} + (n \times p)_{k(j)m} + \epsilon_{(ijklm)n}$, where Y_{ijklmn} = observation, μ = general mean, d_i = effect of diet

($i = 1, 2$), h_j = effect of housing ($j = 1, 2$), $n_{k(j)}$ = effect of nest floor ($k = 1, 2, 3$) within housing j , $(d \times h)_{ij}$ = interaction effect for diet i and housing j , $(d \times n)_{ik(j)}$ = interaction effect for diet i and nest floor k , $\delta_{(ijk)_i}$ = error term for between-subject effects, p_m = effect of feeding phase ($m = 1, 2, 3$), $(d \times p)_{im}$ = interaction effect for diet i and feeding phase m , $(h \times p)_{jm}$ = interaction effect for housing j and feeding phase m , $(n \times p)_{k(j)m}$ = interaction effect for nest floor k and feeding phase m , and $\varepsilon_{(ijkm)n}$ = error term for effect of diet i , housing j , and nest floor k in feeding phase m . Only two repeated factor levels were used in the model for egg quality variables (37 and 68 weeks of age, representing feeding phases 1 and 3, respectively). Bone quality variables and live weights were subjected to analysis of variance using the following model: $Y_{ijkl} = \mu + d_i + h_j + n_{k(j)} + (d \times h)_{ij} + (d \times n)_{ik(j)} + \varepsilon_{(ijk)_i}$, where Y_{ijkl} = observation, μ = general

mean, d_i = effect of diet ($i = 1, 2$), h_j = effect of housing ($j = 1, 2$), $n_{k(j)}$ = effect of nest floor ($k = 1, 2, 3$) within housing j , $(d \times h)_{ij}$ = interaction effect for diet i and housing j , $(d \times n)_{ik(j)}$ = interaction effect for diet i and nest floor k , and $\varepsilon_{(ijk)_i}$ = error term for effect of diet i , housing j , and nest floor k . In Experiment 4, comparisons were made between the control treatment (P16) and the two other treatments with Dunnett's t-test. Residuals were plotted against fitted values to ascertain normality of the data. Transformations were performed when required to attain normality of the data.

In addition, comparisons between the effects of cage types on plumage scores, and bone breaking strength were analyzed over the first three experiments using a mixed model, where the effect of study was considered a random effect and the effect of cage type a fixed effect (St-Pierre 2001).

3 Results and discussion

3.1 General

In all of the experiments and in every treatment the mean cumulative egg production per hen housed was good as it fulfilled the performance goal set by the breeder. A heavy red mite (*Dermanyssus gallinae*) infestation was detected during the last part of Experiment 3 (Period 11). The hen house was treated twice with silica dust, and subsequently, the amount of mites was reduced. Red mite infestation was also detected during Experiment 4, but no treatments other than thorough cleaning were applied. Red mites cause irritation and anemia, may increase mortality, affect egg production, and increase the incidence of blood-stained eggs. Mite-infected hens show more preening, head scratching, feather pecking, and dustbathing than mite-free hens (Kilpinen et al. 2005). However, these mite infestations likely had no major effects on the production results here, as no pronounced decline in production or increase in mortality was observed.

3.2 Interactions between the effects of diet and cage type

Only in the second feeding phase of Experiment 2 was there a statistically significant interaction between the effects of diet and the effects of cage type on any of the production variables. In this case, the low-energy diet decreased the laying rate in CC, whilst it had no such effect in FC. This difference may have been caused by the heavier live weight of hens housed in FC.

Generally, the responses to dietary treatments in Experiments 1–3 were independent of the housing system. This lack of

interaction suggests that no differences in nutrient requirements are present between hens housed in conventional cages and those in small-group furnished cages.

3.3 Diet effects

3.3.1 Egg production and feed consumption

Effects of dietary protein

Hens tend to adjust their feed intake according to their energy requirements; however, if the protein content of the diet is low, birds may increase feed consumption to compensate (Gous et al. 1987). It has also been reported that at the onset of production, dietary protein is the main factor influencing feed intake, and after 23 weeks of age feed energy becomes the main factor determining feed intake (Halle 2002). This can explain the higher feed consumption in groups receiving a low-protein diet during the first feeding phase in Experiment 1 (Study I, Table III).

The lack of effects of dietary protein on laying rate in Experiment 1 suggests that the requirements of protein and amino acids for laying rate were met by both diets. However, the requirements of protein or amino acids for egg weight were not met on the low protein diet in Experiment 1, as in agreement with the findings of Al Bustany and Elwinger (1986), Marsden et al. (1987), and Halle (2002), hens on low-protein diet laid smaller eggs than hens on a high protein diet. In Experiment 1, the low lysine intakes observed in the hens on a low-protein diet may have limited their egg weight, total egg yield, and FCR. Novak et al. (2004) reported increased egg weight with increased daily lysine intake, but no effects on laying rate.

The total sulfur amino acid (TSAA) requirement for FCR estimated by Schutte et al. (1994) (740 mg/hen daily) is in accordance with the results of Experiment 1, where poorer FCR occurred when daily TSAA intake was lower than 740 mg/hen. However, the daily methionine or TSAA intake did not affect FCR in Experiment 3. The lower amino acid intake was accompanied by lower feed consumption, while in Experiment 1 diet had no effect on feed consumption, or feed consumption was higher with a low-protein diet.

Effects of dietary energy

It is well established that hens generally adjust their feed intake according to their energy requirements. This was demonstrated also in Experiment 2, where the hens receiving the low-energy diet consumed more feed than those on the high-energy diet (Study II, Table 2).

The literature contains conflicting results on the effects of dietary energy on laying rate (e.g. Mathlouthi et al. 2002, Çiftci et al. 2003). The finding that increased dietary energy increased laying rate in Experiment 2 (Study II, Table 2) agrees with the results of Keshavartz and Nakajima (1995) and Mathlouthi et al. (2002), but is in contrast to those of Vogt (1986) and Çiftci et al. (2003).

There seems to be a consensus on the lack of effect of dietary energy on egg size (Vogt 1986, Summers and Leeson 1993, Keshavarz and Nakajima 1995, Grobas et al. 1999b, Mathlouthi et al. 2002, Çiftci et al. 2003), with the results of Experiment 2 concurring. When feed energy is increased with a fat supplement, the possible effects on egg size may be accounted for by the fat supplement per se (Vogt 1986, Grobas et al. 1999b) or differences in the body weight of layers (Bish et al. 1985). The effects of a fat supplement on egg weight are attributed to the linoleic acid concentration of the fat supplement. In Experiment 2 the different energy contents of

diets were mainly achieved through the inclusion of different amounts of rapeseed oil, rich in linoleic acid. Despite this, the differences in linoleic acid concentrations of the diets were not very great because of the greater amount of oats, also rich in linoleic acid, included in low-energy diets. In addition, even the low-energy diets in Experiment 2 met the National Research Council's (NRC 1994) requirements of linoleic acid. Thus, the linoleic acid concentrations in low-energy diets were probably so high that no increase in egg weight occurred with increased rapeseed oil and linoleic acid content in the diet.

Effects of dietary calcium

In response to low calcium levels in the diet, hens increase their feed and energy intake (Härtel 1989, Roland and Bryant 1994). However, this response was not evident in Experiment 3. It is likely that the calcium content of both experimental feeds was sufficiently large, and thus, no significant effect on feed consumption emerged.

In Experiment 3, despite the numerically lower feed intake, the hens on the high-limestone diet (HL diet) laid more eggs than their counterparts on the normal-limestone diet (NL diet) over the entire laying period (Study III, Table 4). In agreement with this, Bar et al. (2002) reported an increased laying rate with increased dietary calcium (24 to 49 g/kg feed). In contrast to the findings in Experiment 3, Roland and Bryant (1994) described no effects of increased dietary calcium on the laying rate. The unintended lower methionine content of the HL diet in Experiment 3 restricted the daily methionine intake of the hens on that diet and may partly explain the tendency towards a lower egg weight of these hens.

3.3.2 Egg components and quality

Diet can have effects on both external and internal egg quality (e.g. Al Bustany and Elwinger 1988). Cracked and dirty eggs

cause losses of income to an egg producer. Therefore, factors affecting shell quality have been studied widely (Härtel 1989, Zhang and Coon 1997, Hammershøj and Kjaer 1999, Bar et al. 2002, Keshavarz 2003, Gezen et al. 2005).

Effects of dietary protein

Increased protein content of feed is reported to increase egg size, but impair shell and albumen quality (Al Bustany and Elwinger 1987, Hammershøj and Kjaer 1999). Lower Haugh-unit values detected in eggs from hens on the high-protein diet in Experiment 1 agree with these findings (Study I, Table IV). In Experiment 1 the detrimental effects of high-protein diets on shell percentage were observed only in FC, while no detrimental effect on shell percentage was found in CC. The differences in egg weight did not explain the differences observed in shell percentage.

Effects of dietary energy

In their studies, Keshavarz and Nakajima (1995) and Grobas et al. (2001) found no effects of supplemental fat or increased dietary energy on albumen and yolk weights. This is in agreement with the results of Experiment 2, except for yolk weight assessed at 36 weeks of age, which increased with higher dietary energy (Study II, Table 5). However, Keshavarz and Nakajima (1995) report decreased shell weight with increased energy and constant dietary fat, and increased shell weight with increased fat and constant dietary energy. In Experiment 2, dietary energy was adjusted mainly with rapeseed oil and no effects of diet were observed on shell quality, except in the assessment at 54 weeks of age, when a high-energy diet exhibited increased specific weight and a tendency towards higher shell weight.

Effects of dietary calcium

According to the NRC's Nutrient Requirements of Poultry (1994), the daily calcium requirement of a white egg layer is 3.25 g. However, literature also holds

evidence of higher daily calcium requirements than the NRC (1994) requirements for best shell quality (Bar et al. 2002) and for highest production and specific gravity (Castillo et al. 2004). In Experiment 3, the average daily calcium intake met NRC (1994) requirements in all treatments during each feeding phase (Study III, Table 2), and diet had no significant effects on egg quality (Study III, Table 6).

3.3.3 Health and integument

3.3.3.1 Feather cover

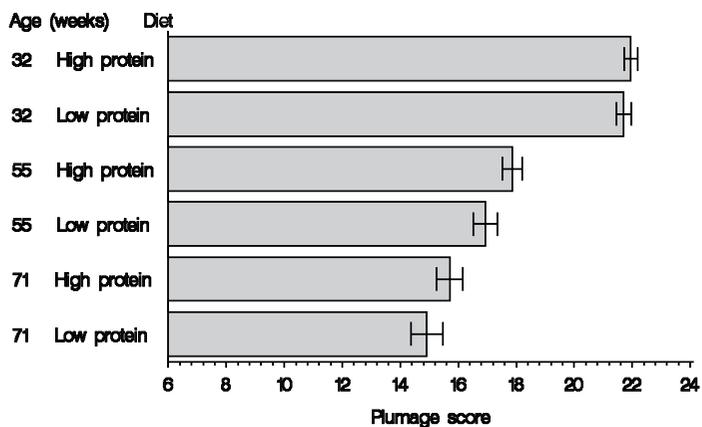
Effects of dietary protein

Protein and amino acid content of feed can affect on plumage condition. Hens on low-protein diets exhibit poorer feather cover than hens on diets with adequate protein (e.g. Al Bustany and Elwinger 1986, 1987, Lund 1991, Ambrosen and Petersen 1997). In addition, methionine-deficient diets result in poorer feather scores (Dänner and Bessei 2002). Feathers are 89–97% protein (Fisher et al. 1981), and about 85% of this protein is keratin (Leeson and Walsh 2004). The most abundant amino acid in feather keratin is cysteine (Leeson and Walsh 2004). In Experiment 1, at the assessments at 55 and 71 weeks of age the hens on the low-protein diet had poorer plumage scores than the hens on the high-protein diet (Figure 4). The connection between low dietary protein and poor plumage condition may be due to increased feather pecking (van Krimpen et al. 2005) or reduced renewal of feathers or both with decreased dietary protein.

Effects of dietary energy

Dietary energy had no significant effects on feather cover in Experiment 2. Al Bustany and Elwinger (1988) reported improved plumage cover when rapeseed was included in a whole cereal mixture diet and attributed this to the higher intake of linoleic acid. In Experiment 2, the dietary energy was adjusted mainly with rapeseed oil, but also with oats. This resulted in a

Fig. 4. Effects of dietary protein on plumage score at various ages in Experiment 1. Means with 95% confidence intervals. The protein (g/kg feed)/energy (MJ/kg feed) ratio was 17 and 13 in the high-protein and low-protein diet series, respectively.



smaller difference in linoleic acid content between the two diets than would have been the case had only the rapeseed oil been used to change the dietary energy.

Effects of dietary calcium

Dietary calcium had no significant effects on feather cover in Experiment 3. No reports on the effects of dietary calcium on the plumage condition were found

3.3.3.2 Footpad lesions

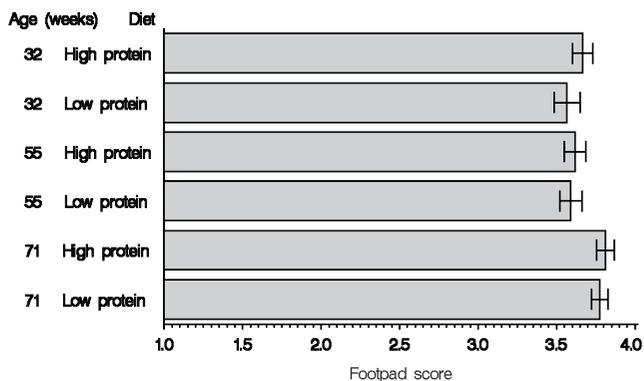
Effects of dietary protein

Low-protein diets have been associated with poorer footpad health (Al Busta-

ny and Elwinger 1986, 1987). In Experiment 1, poorer footpad scores were found in birds on the low-protein diet at the first assessment at 32 weeks of age, but not in the later assessments (Figure 5). The effects of diet on footpad scores may be deduced from excreta wetness and viscosity as sticky droppings, and moisture may predispose birds to footpad lesions (Wang et al. 1998, Mayne 2005).

Dietary treatments in Experiments 2 and 3 had no effects on footpad lesions in this work, and no reports on the effects of dietary energy or calcium on footpad lesions were found.

Fig. 5. Effects of dietary protein on footpad scores at various ages in Experiment 1. Means with 95% confidence intervals. The protein (g/kg feed)/energy (MJ/kg feed) ratio was 17 and 13 in the high-protein and low-protein diet series, respectively.



3.3.3.3 Bone mineralization and strength

Effects of dietary protein

The relationship between dietary protein and bone soundness is controversial (e.g. Darling et al. 2009). On one hand, there is an amino acid requirement to maintain the bone organic matrix and dietary protein may affect bone mineralization through insulin-like growth factor I (IGF-I), but on the other hand dietary protein contributes to acid production and low pH values increase urinary calcium excretion in man and other species (Darling et al. 2009). Rennie et al. (1997) reported no effects of a low-protein layer diet (150 vs. 170 g/kg) supplemented with vitamin K on bone structure and osteoporosis. In agreement with Rennie et al. (1997), no effect of dietary protein on bone-breaking strength emerged in Experiment 1 (Figure 6).

Effects of dietary energy

Jalal et al. (2006) reported no effects of dietary energy on bone ash when dietary energy was between 3 097 and 2 979 kcal/kg. In contrast to this, in Experiment 2, the hens on the low-energy diet had higher bone ash than the hens on the high-energy diet (Figure 7). This is in agreement

with a study on broilers, where a low-energy diet exhibited higher bone ash at the age of 36 days (Venäläinen et al. 2006). In Experiment 2, the dietary energy levels were lower than in the low-energy diet in Jalal et al. (2006), and the difference in energy content between the diets was also greater in Experiment 2 (Study II, Table 1). In addition, the hens on the low-energy diet in Experiment 2 weighed less than the hens on the high-energy diet, while Jalal et al. (2006) reported no differences in live weight. Slower growth rate may increase bone mineralization (Williams et al. 2004).

Although the linoleic acid content in the low-energy diet in Experiment 2 was not much lower than that in the high-energy diet, there was a multifold difference in the ratio of linoleic acid to α -linolenic acid. A higher ratio of dietary linoleic acid to α -linolenic acid has been associated with lower bone mineral density in man (Weiss et al. 2005). High dietary omega-6 fatty acids have been reported to negatively affect bone metabolism in various species (Watkins et al. 2001). It is conceivable that the ratio of dietary linoleic acid to α -linolenic acid explains the dietary effect on bone ash in Experiment 2. In con-

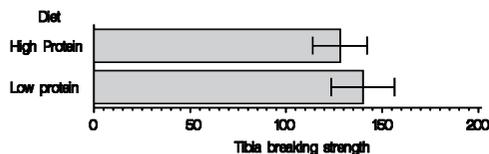


Fig.6. Effects of dietary protein on tibia breaking strength at 73 weeks of age in Experiment 1. The protein (g/kg feed)/energy (MJ/kg feed) ratio was 17 and 13 in the high-protein and low-protein diet series, respectively.

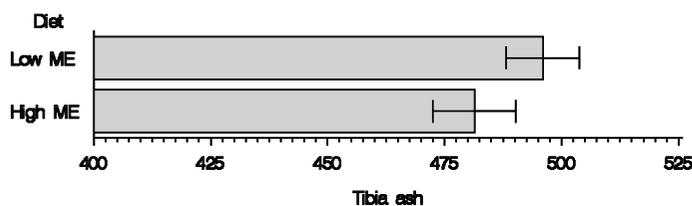


Fig.7. Effects of metabolizable energy (ME) on tibia ash at 73 weeks of age in Experiment 2. The ME contents of the diet series were from 2342 to 2414 kcal/kg feed and from 2581 to 2629 kcal/kg feed in the low-energy and high-energy diet series, respectively.

trast to this, Baird et al. (2008) reported no significant effects of dietary omega-6/omega-3 ratio on layer hens' bone mineral content or tibia strength.

Effects of dietary calcium

The hens on the low-energy diet in Experiment 2 had a lower calcium intake than the hens on the high-energy diet, but this seemed to have no effect on bone ash or bone-breaking strength. In Experiment 3, the higher dietary calcium level resulted in lower bone ash (Study III, Table 5). This was in contrast to the results of Roland et al. (1996), who reported increased bone quality with non-isocaloric diets containing an increased amount of calcium (2.5–5.0%). Excess dietary calcium may reduce the absorption of phosphorus through formation of insoluble calcium phosphate in the intestine (Shafey et al. 1990). In grow-

ing animals, excess calcium or a high calcium-to-phosphorus ratio may disturb bone mineralization (e.g. Hazewinkel et al. 1991, Hurwitz et al. 1995); however, no such evidence appears to exist for laying hens.

3.3.3.4 Mortality and autopsy findings

In the first three experiments, the dead hens were autopsied at the Finnish Food Safety Authority. No statistically significant effects of dietary treatments on mortality rates emerged in Experiments 1 and 3; however, in Experiment 2, a tendency towards a higher mortality in groups receiving the high-energy diet was observed (Study II, Table 2). The frequency data of the causes of death for different dietary treatments in Experiments 1–3 are presented in Table 2.

Table 2. Causes of death during Experiments 1–3 in different dietary treatments.

	Experiment					
	1		2		3	
	Low protein	High protein	Low energy	High energy	High Ca	Normal Ca
Acute heart failure	1	0	1	2	0	2
Cannibalism	0	1	4	6	4	2
Carcinoma	1	0	0	0	0	0
Chronic arthritis	0	0	0	1	0	0
Culled	0	0	1	1	0	0
Fatty liver hemorrhagic syndrome	0	1	6	14	2	5
Intestinal obstruction	0	1	0	0	0	0
Leucosis	0	0	1	1	0	0
Marek's disease	2	0	0	0	0	0
Obstructed crop	0	1	0	0	0	0
Osteomalacia	2	1	0	0	0	0
Prolapsed cloaca	0	0	0	0	0	1
Salpingitis-peritonitis	22	18	5	6	7	3
Sepsis	3	2	3	1	2	0
Trauma	3	0	1	3	5	3
Not diagnosed	6	5	1	2	1	0
Total	40	30	23	37	21	16

In Experiment 2, the greatest difference between the dietary treatments is in the incidence of fatty liver hemorrhagic syndrome (FLHS). This syndrome is caused by a positive energy balance, and other dietary factors, such as high carbohydrate content or excessively low protein or amino acid content, may contribute to induction of FLHS (Butler 1976). In Experiment 2, calculated daily energy intakes did not differ between the diets (Study II, Table 2), but hens on the high-energy diet were heavier than hens on the low-energy diet (Study II, Table 3), and thus, predisposed to FLHS. Schumann et al. (2000) suggest that dietary linolenic acid may diminish the amount of fat deposited in the liver of laying hens, but on the other hand omega-3 fatty acids may increase the possibility of hemorrhage in the avian liver.

3.4 Effects of cage type

3.4.1 Egg production and feed consumption

No significant differences were present in egg production between the cage types in Experiment 2. However, a significant difference in egg production between the cage systems was detected in Experiments 1 and 3, in favor of the conventional cages. This is in agreement with the study of Glatz and Barnett (1996) with cages equipped with perches, but in contrast to several reports of equal egg production in conventional and fully furnished cages (e.g. Abrahamsson et al. 1995, Abrahamsson and Tauson 1997, Appleby et al. 2002, Guesdon and Faure 2004).

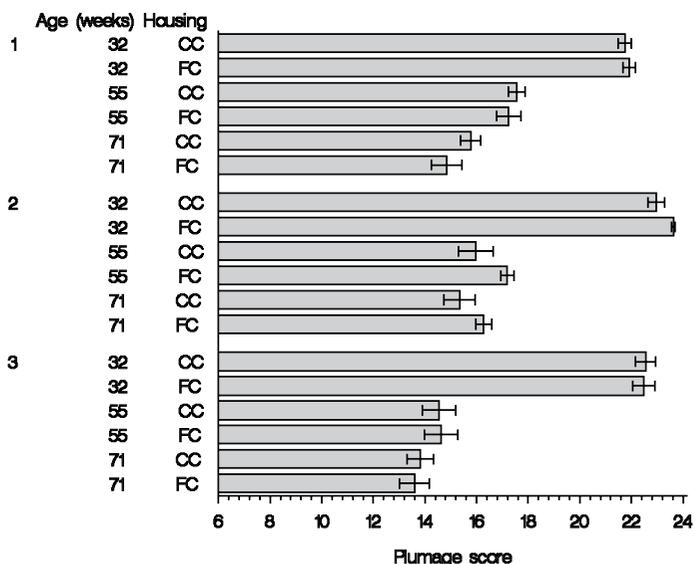
The effects of cage type on feed consumption were inconsistent between the three experiments (1–3). In Experiment 1, feed consumption was constantly lower in FC than in CC (Study I, Table III). However, in Experiment 2, feed consumption in FC was higher during the first feeding phase, but lower during the last feeding phase

in comparison with CC. In Experiment 3, feed consumption differed significantly between the cage types during the second feeding phase, being lower in FC.

Feed consumption closely follows the energy requirements of the hen. Thus, live weight, feather cover, activity, and production affect individual feed consumption of hens within a flock, in the same environment (McDonald 1978, Tauson and Svensson 1980, Peguri and Coon 1993). Higher live weight in FC at the beginning of Experiment 2 may explain the higher feed consumption in FC during the first feeding phase. The plumage scores in Experiments 1–3 comparing conventional and furnished cages do not explain the differences in feed consumption very well. Only in Experiment 2, at the third assessment (at 71 weeks of age), did groups with higher plumage scores have lower feed consumption during the corresponding feeding phase (see Section 3.4.3.1, Figure 8 for plumage scores). The lack of effect on feed consumption may be accounted for by the relatively small differences in plumage scores. When the difference between the mean total scores is around one point, such a difference in feather cover may be insufficiently large to significantly affect heat loss and feed consumption in these circumstances.

In all, there seems to be a tendency in FC towards lower feed intake than in CC, despite the existence of such factors as larger group size and total cage area per hen (Carey et al. 1995), which could increase bird activity and feed intake in FC. This tendency may arise from the effects of perches, as was seen in Experiment 4, where the presence of perches diminished feed consumption during the prelaying period and enhanced FCR during the early laying period. Perches in cages have been reported to diminish bird activity (Braastad 1990, Matsui et al. 2004). In addition, energy savings may be explained by crowding of birds on the perch, result-

Fig.8. Plumage scores of hens in conventional (CC) or furnished (FC) cages at three assessments (32, 55, and 71 weeks of age) in Experiments 1–3. Means with 95% confidence intervals. Range of plumage score is from 6 to 24, with higher score indicating better condition.



ing in less heat losses (Tauson and Jansson 1988). As no significant differences emerged in feed consumption in Experiment 4 after the prelaying period, the decreased feed consumption in FC compared with CC could also be attributed to the presence of wood shavings, due insoluble fiber, which has beneficial effects on nutrient digestion (Hetland and Svihus 2001, Hetland et al. 2003a). However, Hetland and Svihus (2007) reported that even though apparent metabolizable energy (AME) value of feed was enhanced when wood shavings were available, there were no effects of wood shavings on feed consumption. The authors concluded that the enhanced utilization of nutrients was used to cover the grinding and handling costs of wood shavings in the gastrointestinal tract. In the present work, the wider feed trough space per hen in conventional than in furnished cages may partly explain the higher feed consumption observed in CC, as increased feeder space per hen has been reported to increase feed consumption (Hill and Hunt, 1980). It is possible that the absence of any other loose material to peck and use as a dust-bathing substrate also increased feed wastage in CC,

but no means to record feed wastage separately from feed consumption was available during the experiments.

The most important factor affecting the profitability of egg production is FCR. The cage system had no significant effects on FCR in Experiments 1–3. Because there were no differences in FCR between the cage types, it may also be argued that the lower feed intake in FC than in CC is a result of lower egg production, and thus, lower energy requirements of the hens housed in FC.

3.4.2 Egg quality

Lower specific gravity was found in eggs from FC than in those from CC in Experiments 1–3 in at least one of the assessments. Shell-breaking strength was lower in FC than in CC in one or two assessments in Experiments 1 and 2 (Studies I and II), but not in Experiment 3 (Study III). This implies that specific gravity is a more sensitive indicator of shell calcification or that specific gravity has a smaller variance than breaking strength as it was measured in these experiments.

During each experiment egg quality reports were received weekly from the packing plant, separately for each treatment. These data were not analyzed statistically, as only one observation per treatment was available each week. Sums of egg grading results were calculated for each experiment. The proportions of class A, cracked, and dirty eggs are presented in Table 3. All eggs, except those with leaking cracks and shell-less eggs, were sent to the packing plant.

The proportion of cracked eggs was greater in CC than in FC in Experiments 1–3. In Experiment 3, the difference between cage types was smaller because there were more cracked eggs from cages with smooth plastic nest flooring (6.23%) than from cages with artificial turf nest flooring (4.51%). The proportion of dirty eggs was smaller in CC than in FC in Experiments 1–3. About equal proportions of class A eggs were obtained from the two cage types.

The greater proportion of cracked eggs from CC was contrary to expectations based on earlier studies (e.g. Abrahamsson et al. 1995, Abrahamsson and Tauson 1997, Wall et al. 2002, and Guesdon and Faure 2004). Cage design may affect incidence of cracked eggs. The furnished cages used had a relatively gentle floor inclination (10%) relative to the 14% slope allowed by Council Directive 1999/74/EC (Commission of the European Communities 1999). The slope in CC was 12%. In

addition to floor inclination, nest design and location affects the risk of egg cracking (Tauson 2005). In the furnished cage model, the nest covered the entire depth of the cage. As the proportion of cracked eggs was also greater in FC with smooth perforated plastic nest flooring than in FC with artificial turf nest flooring, it seems that artificial turf has properties that protect eggs from cracks. One factor may simply be that eggs laid in nests are better protected. Guesdon et al. (2006) reported that eggs laid outside of the nests were more prone to cracks than eggs laid in the nests. In addition, there is less rolling friction between the egg shell and a rigid smooth plastic floor than between the egg shell and artificial turf. Greater rolling friction in nests with artificial turf will slow down the rolling speed of eggs and diminish the collision forces.

3.4.3 Health and integument

3.4.3.1 Feather cover

Figure 8 presents the effects of cage type on plumage score in Experiments 1–3. Differences in plumage condition between the cage types were statistically significant at every assessment in Experiment 2, where hens in FC got higher scores than hens in CC. However, in Experiment 1, hens in CC got higher scores at 71 weeks of age. In the third experiment, plumage scores did not differ significantly between the cage types. The factors affecting feather cover

Table 3. Proportions of various egg grades during 52-week laying period in conventional (CC) or furnished (FC) cages in Experiments 1–3, and cages with artificial turf (AT) and cages with smooth perforated plastic (PP) in Experiment 3.

	Experiment							
	1		2		3		3 (FC)	
	CC	FC	CC	FC	CC	FC	AT	PP
Grade	%							
Class A	93.2	94.9	90.2	93.2	90.5	90.5	91.1	89.8
Cracked	4.31	2.51	6.42	3.71	6.46	5.37	4.51	6.23
Dirty	1.95	2.32	2.44	2.63	2.48	3.65	3.94	3.36

and possible reasons behind the conflicting results on plumage scores include nutrition, air humidity, the incidence of feather pecking and the amount of abrasion (Tauson 1986). Based on the data from these three experiments (1–3) analyzed together, the difference in plumage scores between the cage types studied was not statistically significant.

The three different perch designs used in Experiments 1 and 2 had no effect on plumage scores.

3.4.3.2 Footpad and keel bone lesions

The incidence of bumble foot (pododermatitis) was higher in furnished than in conventional cages in Experiments 1–3 (Figure 9). This was expected based on the

literature. The incidence of bumble foot has been related to the presence of a perch (e.g. Abrahamsson et al. 1996, Appleby et al. 1993, Tauson and Abrahamsson 1994), and the results from Experiment 4 support this view (Study IV, Table 3). Similarly, the results from Experiment 4 support the idea that the occurrence of hyperkeratosis is related to time spent on an inclined wire floor (Abrahamsson et al. 1996, Abrahamsson and Tauson 1997) and is diminished in the presence of perches. Keel bone deformation has also been related to the presence of a perch (Appleby et al. 1993, Tauson and Abrahamsson 1994, Abrahamsson et al. 1996), and the higher incidence of severe deformations in FC than in CC in this work is consistent with this view (Figure 10).

Fig.9. Footpad scores of hens in conventional (CC) or furnished (FC) cages at three assessments (32, 55, and 71 weeks of age) in Experiments 1–3. Means with 95% confidence intervals. Range of footpad scores is from 1 to 4, with higher score indicating better condition.

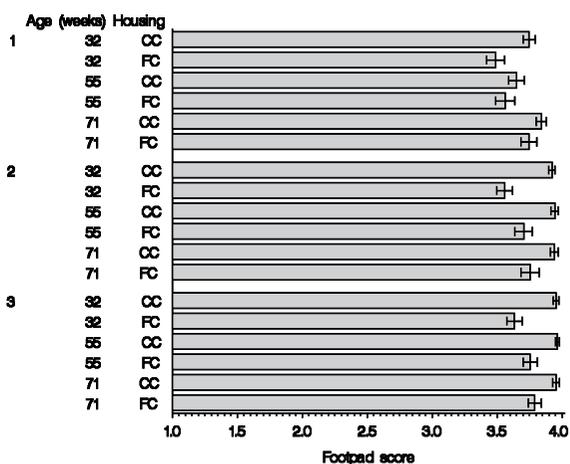
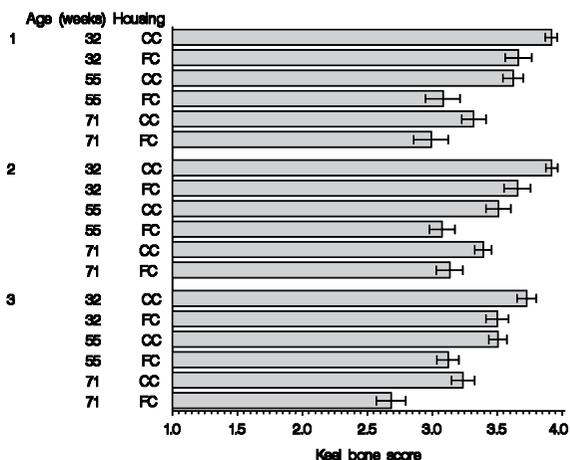


Fig.10. Keel bone scores of hens in conventional (CC) or furnished (FC) cages at three assessments (32, 55, and 71 weeks of age) in Experiments 1–3. Means with 95% confidence intervals. Range of keel bone scores is from 1 to 4, with higher score indicating better condition.



Effects of perch design

The hens in cages equipped with plastic perches had a higher incidence of bumble foot than the hens in cages with the two wooden perch designs (Figures 11 and 12) at 55 and 71 weeks of age in Experiments 1 and 2. This finding agrees with the results of Tauson and Abrahamsson (1994).

However, in the current work, the effects of perch material and shape cannot be separated, as the three perch designs differed in both shape and material. No significant differences were seen in the incidence of keel bone lesions between the three perch designs.

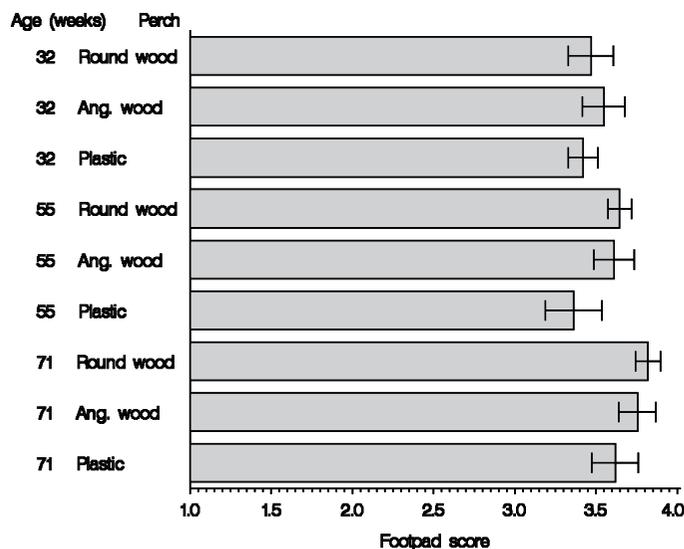


Fig.11. Footpad scores of hens in furnished cages equipped with wood perches with round cross-section (Round wood), wood perches with angular cross-section (Ang. wood), or plastic perches with T-shaped cross-section (Plastic) at three assessments (32, 55, and 71 weeks of age) in Experiment 1. Means with 95% confidence intervals. Range of footpad scores is from 1 to 4, with higher score indicating better condition.

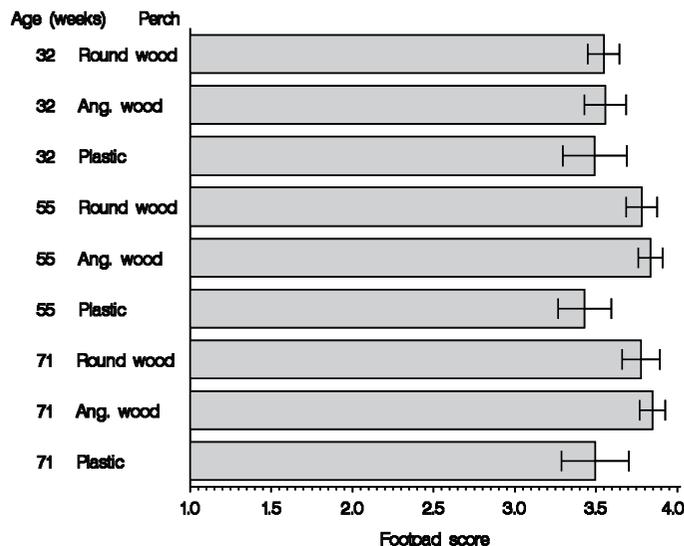


Fig.12. Footpad scores of hens in furnished cages equipped with wood perches with round cross-section (Round wood), wood perches with angular cross-section (Ang. wood), or plastic perches with T-shaped cross-section (Plastic) at three assessments (32, 55, and 71 weeks of age) in Experiment 2. Means with 95% confidence intervals. Range of footpad scores is from 1 to 4, with higher score indicating better condition.

3.4.3.3 Bone mineralization and strength

Tibia ash was assessed at the end of Experiments 2 and 3. In both experiments, the tibia ash content was greater in FC than in CC ($P < 0.05$) (Figure 13). This finding agrees with Jendral et al. (2008) and Tactacan et al. (2009), who reported higher tibia mineral density in furnished than in conventional cages. Lack of exercise in CC may contribute to loss of bone minerals (Leyendecker et al. 2005). The type of activity influences skeletal adaptation (Bennell et al. 1997). Stepping up on a perch may produce a greater mechanical stimulus than walking on a floor, thus enhancing bone mineralization. However, tibia breaking strength assessed at the

end of Experiments 1–3 showed no response to the housing system (Figure 14). The tibia breaking strength had a high random variation, and thus, it was less sensitive to changes in housing or diet than tibia ash content. Hughes and Appleby (1989), Duncan et al. (1992), and Jendral et al. (2008) reported higher tibia breaking strength in cages furnished with perches than in conventional cages.

3.4.3.4 Mortality and autopsy findings

The frequency data of the causes of death for the two cage types in Experiments 1–3 are presented in Table 4. In Experiments 1–3, some cannibalism cases occurred in both cage types. The most prevalent cause

Fig.13. Tibia ash content (g/kg DM) of hens in conventional (CC) or furnished (FC) cages at the end of Experiments 2 and 3 (at 72 weeks of age). Means with 95% confidence intervals.

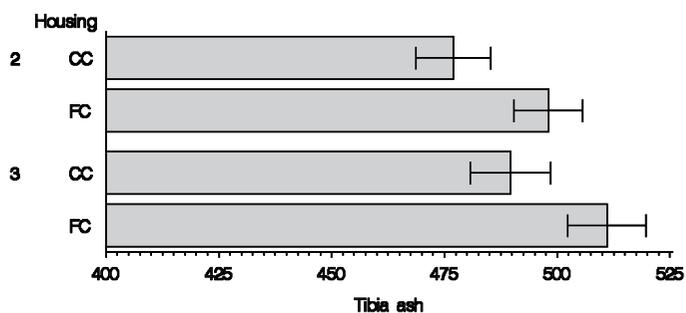


Fig.14. Tibia breaking strength (N) of hens in conventional (CC) or furnished (FC) cages at the end of Experiments 1–3 (at 72 weeks of age). Means with 95% confidence intervals.

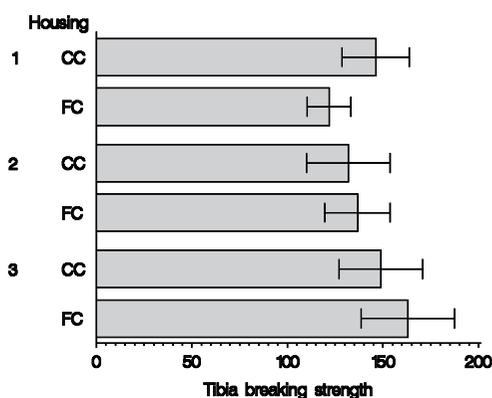


Table 4. Causes of death in conventional (CC) and furnished (FC) cages during Experiments 1–3.

	Experiment					
	1		2		3	
	CC	FC	CC	FC	CC	FC
Acute heart failure	0	1	2	1	2	0
Cannibalism	0	1	6	2	3	3
Carcinoma	1	0	0	0	0	0
Chronic arthritis	0	0	1	0	0	0
Culled	0	0	1	1	0	0
Fatty liver hemorrhagic syndrome	0	1	8	12	3	4
Intestinal obstruction	0	1	0	0	0	0
Leucosis	0	0	1	1	0	0
Marek's disease	1	1	0	0	0	0
Obstructed crop	0	1	0	0	0	0
Osteomalacia	3	0	0	0	0	0
Prolapsed cloaca	0	0	0	0	1	0
Salpingitis-peritonitis	21	19	8	3	2	8
Sepsis	3	2	1	3	1	1
Trauma	1	2	4	1	0	8
Not diagnosed	6	5	2	1	1	1
Total	36	34	34	25	13	25

of death was, however, salpingitis-peritonitis. Peritonitis is characterized by exudate on serosal surfaces either locally or widely spread throughout the body cavity (Trampel et al. 2007). In salpingitis, exudate is found in the oviduct, mainly within the magnum (Jordan et al. 2005). These exudates vary in color from cream to yellow and brown (Jordan et al. 2005). Salpingitis-peritonitis is thought to be caused by *Escherichia coli* (Jordan et al. 2005, Trampel et al. 2007). However, unknown predisposing factors may play a part in infection (Jordan et al. 2005).

3.5 Behavior in furnished cages

3.5.1 Use of facilities

Birds' use of facilities was not reported in Studies I–III. A summary of the data from the corresponding experiments (1–3) is presented in Figures 15–19. Both nests

and perches were extensively used in each experiment, as expected from earlier reports (Appleby and Hughes 1995, Abrahamsson et al. 1996, Abrahamsson and Tauson 1997). The proportion of eggs laid in nests was constantly high in Experiments 1 and 2, being about 98%. In Experiment 3, this proportion was lower because the nest floor material significantly ($P < 0.001$) affected the proportion of nest eggs (see Section 3.5.1.2).

The proportion of hens perching during the daytime varied between 31% and 49% (data not shown), being higher than the 28% reported by Abrahamsson and Tauson (1997) in their study with LSL hens and a perch length of 12 cm per bird. On the other hand, during nighttime inspections (Figure 15) the proportion of hens perching was lower here than the 91% reported by Abrahamsson and Tauson (1997).

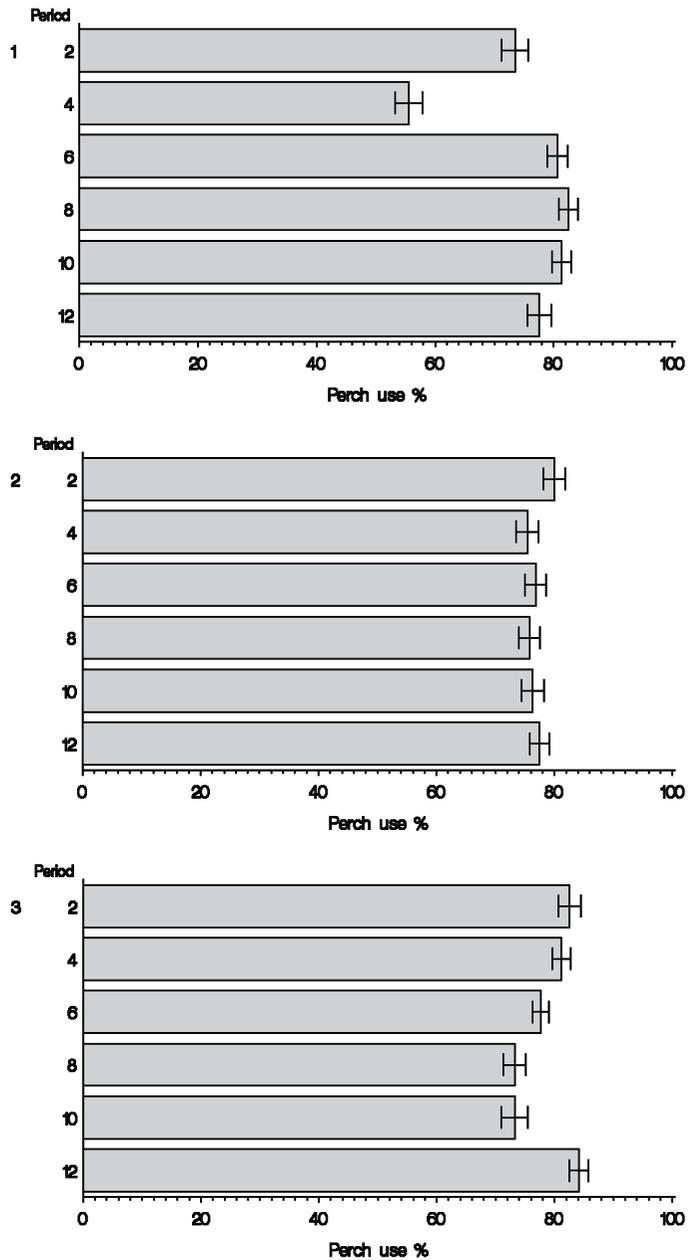


Fig. 15. Proportion of birds perching during scan observations at 1 h after lights-out in Experiments 1–3. Means with 95% confidence intervals.

Nests were also used for roosting (Figure 16). The proportion of hens in the nest during the scan observations at 1 h after lights-out was considerably higher in all experiments in this work than in Abrahamsson and Tauson (1997) or Wall and Tauson (2002). Wall and Tauson (2007) noted that white hybrids were more prone

to roost in nests than brown hybrids. Some hens may simply prefer the nest, but there may also be social factors affecting the choice of roosting place. The significant differences observed in the proportion of hens in the nest during the scan observations at 1 h after lights-out between the sampling times (periods) may be related to

hens' age, as the proportion seems to increase with time in Experiments 1 and 2 (Figure 16). Changes in ambient temperature may also affect the choice of roosting place, as resting side by side conserves heat in cold temperatures, but may be uncomfortable in warm temperatures.

During the first experiment no entry to the litter area was observed during the recordings of birds' location. The birds in Experiment 1 were allowed into the litter area from the age of 21 weeks, and this may have affected their later behavior. Birds in Experiments 2 and 3 were allowed in the litter area at 16 or 17 weeks of

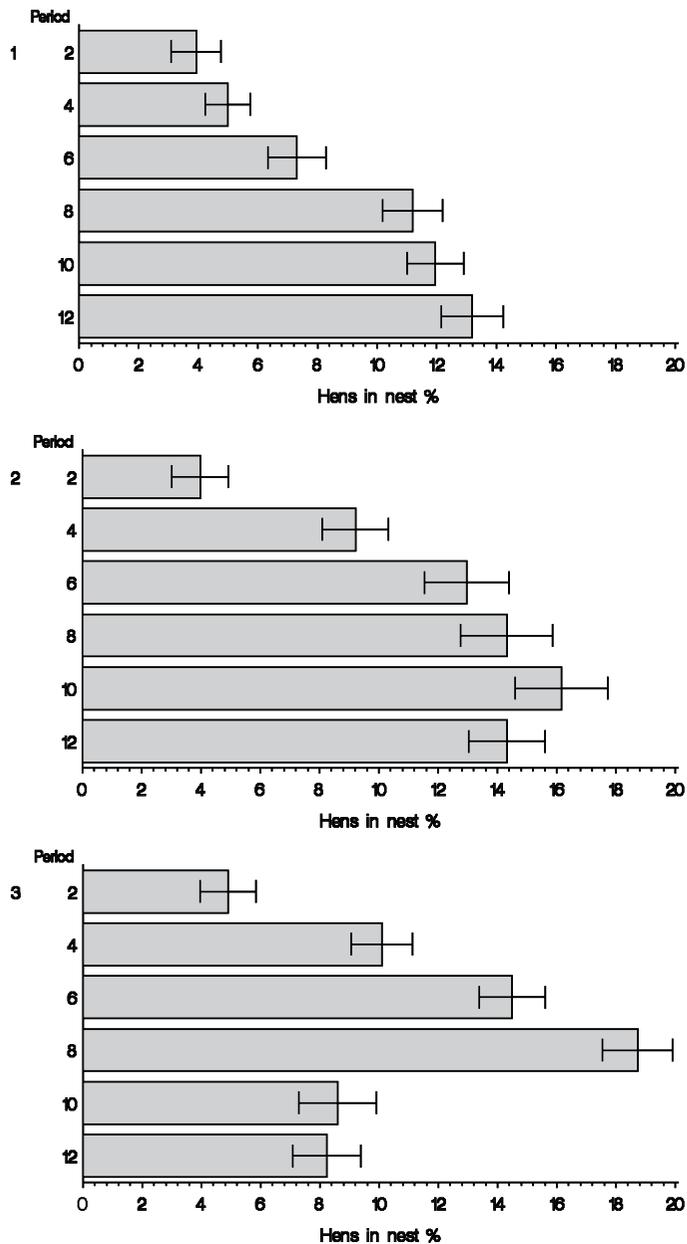


Fig. 16. Proportion of birds in the nest during scan observations at 1 h after lights-out in Experiments 1–3. Means with 95% confidence intervals.

age, and more frequent use of the litter box was observed in these experiments (Figure 17). In the first experiment, the litter boxes were opened daily at 9.5 h after lights-on, while in Experiments 2 and 3 they were opened 1 h earlier (8.5 h after lights-on). According to Vestergaard (1982), initiation of dustbathing peaks at 6–7 h after lights-on, and the overall mean duration of a dustbathing bout is 27 min. The use of the litter box in the present work may have been sparse during the scan observations because litter boxes were opened later than the proposed peak in hens' dustbathing behavior and because in Experiments 1–3 the first observations were made 30 min after opening of the litter boxes. In Experiment 4, where individual birds were observed, most of the sham dustbathing bouts oc-

curred before the litter box was opened. Thus, the use of the litter box might have been more frequent had the opening hour been earlier.

In several studies, hens have used litter areas in FC infrequently (e.g. Abrahamsson et al. 1996, Lindberg and Nicol 1997, Olsson and Keeling 2002), even though it is established that hens are motivated to dustbathe and are willing to work to gain access to litter (Widowski and Duncan 2000, de Jong et al. 2005). Several reasons for the restricted use of the dustbath have been suggested: litter in dustbath may be quickly depleted, dustbaths may be empty most of the time (Lindberg and Nicol 1997), and competition may occur for the limited dustbathing area (Abrahamsson

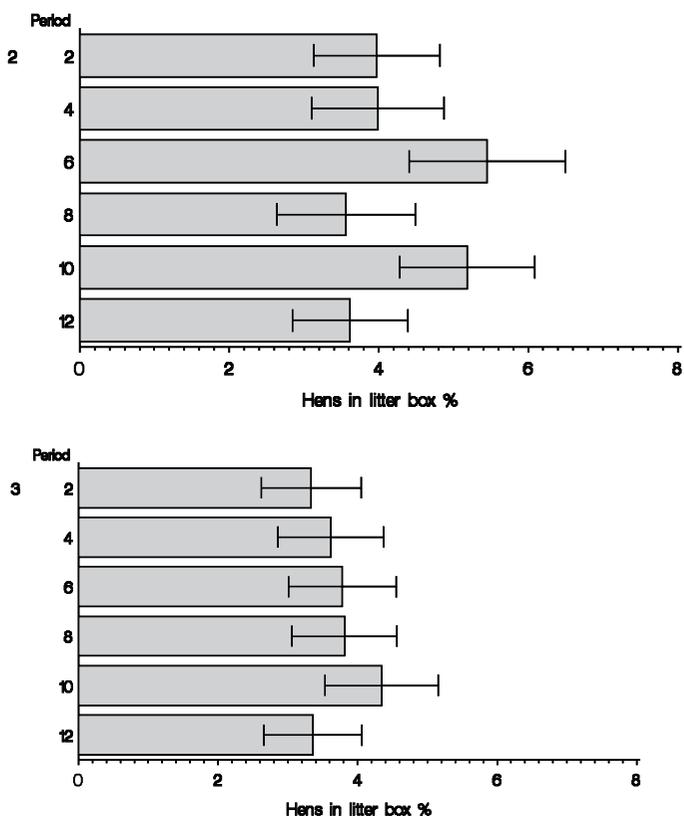


Fig. 17. Proportion of birds in the litter box during scan observations at 30 min after the opening of the litter area in Experiments 2 and 3. Means with 95% confidence intervals.

et al. 1996, Shimmura et al. 2007a). Ease of access may also be of importance for the use of the litter area (Olsson and Keeling 2002).

3.5.1.1 Effects of perch design

Three different perch designs were compared in Experiments 1 and 2. The two wooden perches were compared with a plastic perch, and the two wooden perches with different cross-sections were compared with each other. No statistically significant effects of perch design on proportion of nest eggs emerged. In agreement with the findings of Tauson and Abrahamsson (1994) and Lambe and Scott (1998), who reported no differences in the use of different perch designs, there were no effects of perch design on the proportion of hens on perches or in nests during the daytime or nighttime inspections.

3.5.1.2 Effects of nest flooring

Two different nest floorings were compared in Experiment 3. In cages with an artificial turf nest floor, about 98% of eggs were laid in nests, but in cages with smooth perforated plastic (PP) nest flooring, about 90% of eggs were laid in nests.

rated plastic nest flooring only 90% of eggs were laid in nests (Figure 18).

Guesdon and Faure (2004) reported a greater proportion of eggs laid in nests in cages with Astro-turf than in cages with thin plastic mesh lining, and Struelens et al. (2005) stated that hens preferred artificial turf and peat to coated wire mesh. Wall et al. (2002) reported a lower proportion of nest eggs when the area of the artificial turf nest lining was reduced to 30% or 50% than when 100% of the nest floor was lined. Reed and Nicol (1992), on the other hand, reported that a small strip of artificial turf was enough to attract hens to spend more time in the nest and encourage nesting behavior. The perforated plastic nest floor in Experiment 3 was not as attractive as artificial turf based on the proportion of nest eggs. The reason for this may be that smooth and stiff plastic is not manipulable at all, while artificial turf, even if it is fixed and cannot be moulded, can be pulled, pecked, and scratched. However, in Experiment 4, where similar smooth plastic nest floors were used, the proportion of nest eggs was higher: 95–98%.

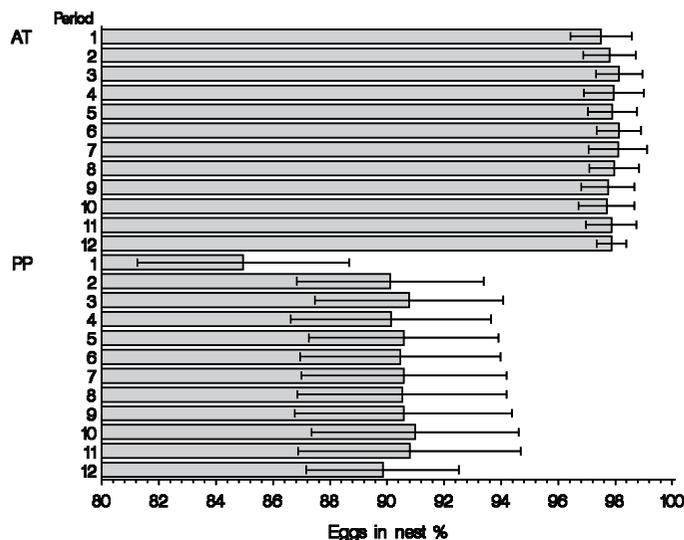


Fig. 18. Proportion of eggs laid in nests during Experiment 3 in cages with either artificial turf (AT) nest flooring or smooth perforated plastic (PP) nest flooring. Means with 95% confidence intervals.

In Experiment 3, during the scan observations in the dark (1 h after lights-out) there was a significant interaction between the effects of period and the effects of nest flooring ($P < 0.001$) on the proportion of hens in nests (Figure 19). In period 2, the proportion of hens roosting in nests was smaller in cages with perforated plastic (PP) flooring than in cages with artificial turf (AT) nest floors. In scan observations during periods 4–8, no differences between the nest floorings were observed, while in observations during periods 10 and 12, more hens were roosting in nests in cages with PP floors than in cages with AT floors.

3.5.2 Effects of presence of perches on hen behavior

Experiment 4 studied the effects of perches on performance and behavior of hens. We hypothesized based on the literature (Braastad 1990, Matsui et al. 2004) that the presence of perches would make hens less active. According to the observations

of individual birds during the light period, the birds without access to perches sat less frequently, but were recumbent more often relative to those with access to perches. During the recordings of bird location at 1 h after lights-out, the birds without perches tended to more frequently be in nests than those with perches. Use of the nest as a roosting place may increase soiling of the nest, thus increasing the incidence of dirty eggs (Abrahamsson et al. 1995). However, the small number of replicates of behavior observations on individual birds ($n=3$) diminished the power of the statistical test in the Study IV. Small power results in an increased risk of false acceptance of H_0 (meaning that there is an actual difference between the treatments, but it is not detected with the test). The risk of false acceptance of H_0 was greater than the risk of false rejection of H_0 . Based on the results Experiment 4, we could not unequivocally conclude that the presence of perches diminishes the activity of hens, despite some significant differences in resting behavior.

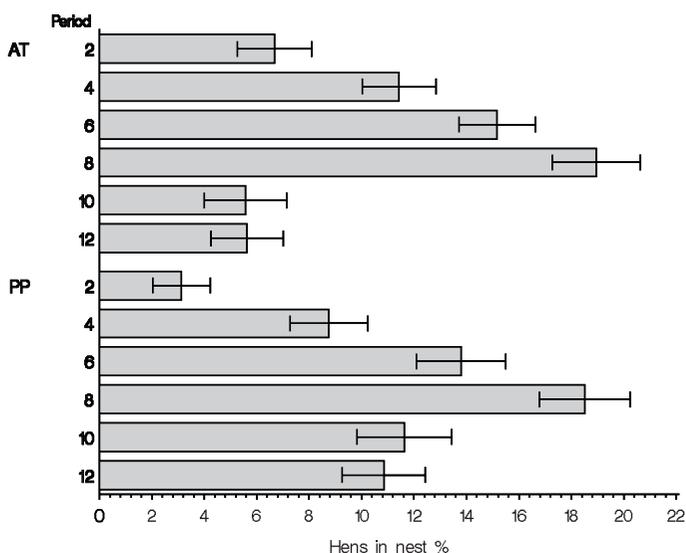


Fig. 19. Proportion of birds in the nest during scan observations at 1 h after lights-out in cages with either artificial turf (AT) nest flooring or smooth perforated plastic (PP) nest flooring in Experiment 3. Means with 95% confidence intervals.

4 Concluding remarks and practical application of the results

The following conclusions and practical applications based on Experiments 1–4 and the results reported in the literature can be tendered for laying hens in small-group furnished cages.

1. Production performance comparable with conventional cages can be achieved in furnished cages. There was no evidence supporting a change in nutrient requirements for laying hens when conventional cages are replaced with small-group furnished cages. The results from nutritional experiments conducted in conventional cages can be applied to small-group furnished cage systems.
2. The daily requirements of protein and amino acids for egg weight and feed conversion ratio seem to be higher than the NRC (1994) requirements for Leghorn-type laying hens.
3. Hens respond to low-energy diets by increasing their feed intake. Low-energy diets may restrict laying rate, but do not affect energy efficiency.
4. Increased dietary limestone did not restore egg shell breaking strength in furnished cages. This implies that the weaker shells observed in furnished cages are not caused by a higher amount of calcium being retained in bones.
5. Measures to encourage laying in nests may diminish the proportion of cracked eggs. Measures to encourage roosting on perches during nighttime will decrease the proportion of hens spending the night in nests.
6. Hens accept a variety of raised structures as perches and quickly learn to use perches even without prior experience. The incidence of pododermatitis is greater with plastic than with wooden perches.
7. All of the advantages of cages for bird welfare are sustained in the small-group furnished cages. In addition, there are other benefits for bird welfare in these cages. Frequent use of perches and nests imply a wider behavioral repertoire in furnished cages than in conventional cages, and this can be perceived as a welfare benefit. Moreover, the increase in bone-breaking strength may improve bird welfare. However, the available area is still rather restricted.
8. These results cannot be generalized to furnished cages housing large groups of hens. Thus, further research is needed with large-group furnished cages. Another restriction for generalization is the use of only one hybrid in the present work. Hybrids may differ in their responses to diet and environment. These differences should be investigated. The effects of different pullet rearing environments also warrant continued research, as prior experience may affect behavior later in life. An important practical problem requiring elucidation is the proportion of dirty and cracked eggs in FC. Based on the present work, egg shells are weaker in furnished cages than conventional cages, but the reason for this remains unclear.

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