Effect of low-density diets on broiler breeder and offspring performance

Henk Enting

Proefschrift

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Stellingen

1. Minder geconcentreerde (opfok)voeders voor vleeskuikenouderdieren verbeteren de eisamenstelling, de embryonale ontwikkeling en de vitaliteit van de nakomelingen (dit proefschrift).

2. Het verstrekken van minder geconcentreerde voeders aan vleeskuikenouderdieren verbetert het welzijn alleen gedurende de eerste helft van de opfokperiode (dit proefschrift).

3. Het feit dat de voergift bij vleeskuikenouderdieren met meer dan 50 % moet worden beperkt voordat een duidelijke toename van het corticosterongehalte in het bloed wordt waargenomen, geeft aan dat de *ad libitum* voeropname van deze dieren te hoog is en niet als referentie kan worden gebruikt om de mate van voerbeperking te beschrijven (De Jong et al., 2003).

4. In de literatuur krijgt de invloed van de dooier en de benutting van vetten daaruit op de embryonale ontwikkeling van vleeskuikens te veel aandacht. Het verbeteren van de ontwikkeling van de embryonale darm is waarschijnlijk veel belangrijker voor de ontwikkeling van embryo en kuiken (Noble et al., 1986a&b; Yaffei en Noble, 1990; Vajda et al., 1994).

5. Management staat veelal inspirerend en stimulerend leiderschap in de weg.

6. De opmerking 'dat is onvoldoende gecommuniceerd' wordt dikwijls verward met een 'incompatabilité d'humeur'.

7. Survivaltochten en nachtelijk cafébezoek zijn een onderschat middel bij het verkrijgen van inzicht in de kracht van een team en de individuen in dat team.

Stellingen behorende bij het proefschrift
'Effect of low-density diets on broiler breeder and offspring performance'
Henk Enting, Wageningen, 24 juni 2005

Abstract

Restricted feeding of broiler breeders is required to obtain good reproductive performance. Current practical feed restriction levels can result in hunger feeling and chronic stress, particularly during the rearing period. On the basis of literature data, low-density diets might improve bird welfare. Recent findings also indicate that low-density broiler breeder diets can reduce offspring mortality. In this thesis, effects of low-density breeder diets on bird welfare and breeder and offspring performance were evaluated. Breeder treatments involved: 1) normal density diets (ND), 2) diets with 12 and 11 % reduced nutrient densities during rearing and laying (LD12 and LD11), 3) diets with 23 and 21 % reduced nutrient densities during rearing and laying (LD23 and LD21), 4) as 2), but with oats and sugar beet pulp instead of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal in the diets ($LD12^{OP}$ and $LD11^{OP}$), and 5) LD11 diets during rearing followed by ND diets during laying.

Feeding LD23 diets reduced stereotypic pecking behaviour and increased time spent on sitting during the first half of the rearing period. LD23 and $LD12^{OP}$ diets reduced feed intake motivation during rearing. It was concluded that LD23 can improve bird welfare during the first half of the rearing period. However, LD21 impaired bird welfare during laying.

$LD12^{OP}$ and $LD11^{OP}$ diets gave significantly lower live weights during rearing and laying. Low-density diets delayed reproductive tract development at 24 weeks of age, which was followed by an increased development between week 24 and 26. Changes in bird development were related to changes in nutrient digestibility and utilization of digested nutrients. Egg weights and amount of egg white increased and embryonic development was improved on low-density diets. Laying percentage was significantly higher on LD11 diets. LD11 diets increased live weight of offspring of 29-week-old breeders significantly in comparison with ND diets. Low-density breeder diets resulted in a significant reduction in offspring mortality when breeders were 60 weeks of age. Antibody titres in offspring indicated that nutrients in eggs with a relatively low weight were used for growth rather than for immune system development. It was concluded that low-density broiler breeder diets can improve offspring performance and offspring vitality.

Voorwoord

Het onderzoek dat in dit proefschrift is beschreven is het resultaat van een project dat door De Schothorst en ID-Lelystad is uitgevoerd. Bij de uitvoering van dit onderzoek waren meerdere personen en instanties betrokken, die ik hierbij hartelijk wil danken voor hun bijdrage. Het onderzoek werd gefinancierd door het Ministerie van Landbouw, Natuurbeheer en Visserij, het Productschap Diervoeder en de Productschappen Vee, Vlees en Eieren. Het bestuur van Schothorst Feed Research en Piet van der Aar wil ik bedanken voor de mogelijkheid dit promotieonderzoek op De Schothorst uit te voeren. Binnen het project is vanuit ID-Lelystad met name door Ingrid de Jong en Theo Kruip veel werk verzet en met hen is bijzonder plezierig en voortvarend samengewerkt. Helaas heeft Theo na afloop van het project slechts korte tijd van zijn VUT kunnen genieten.
Naast Ingrid de Jong en Theo Kruip hebben ook met groot aantal andere personen van ID-Lelystad een bijdrage geleverd aan het onderzoek. Renze Borger, Agnes de Wit en Leo Kruijt hebben de eisamenstelling en de ontwikkeling van de embryo's bestudeerd. Jan Cornelissen en Wim Boersma hebben de zorg gedragen voor het vaststellen van de IgM en IgG titers. Annemarie Rebel heeft het effect van een malabsorptie-infectie op groei en miltontwikkeling vastgesteld. Sander Lourens heeft eveneens een grote bijdrage aan het onderzoek geleverd door te zorgen voor het uitbroeden van de eieren voor de vleeskuikenproeven.
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Henk

Contents

Chapter 1

General Introduction

Introduction

In current practice, broiler breeders are fed restrictedly during the rearing and laying period. The level of feed intake restriction can exceed 50 % of the ad libitum feed intake during the rearing period (Savory and Kostal; De Jong et al., 2002). The restriction of feed intake is applied for two reasons. One reason is that restricted fed broiler breeders lay substantially more hatching eggs than ad libitum fed birds (Katanbaf et al., 1986; Hocking et al., 1994; Decuypere et al., 1999), thus giving less offspring. This is associated with changes in hormone levels that are involved in the process of onset of lay and of maintaining egg production (Bruggeman, 1998; Renema et al., 1999). The other reason to restrict feed intake is the lower live weight and higher activity of restricted fed broiler breeders compared with ad libitum fed birds. This means that less feed is needed to meet maintenance requirements and that a higher percentage of fertilized eggs is obtained due to the higher activity of male and female birds.

There are indications that current levels of feed intake restriction impair broiler breeder welfare. In a number of studies, changes in behaviour and stress physiology have been observed that are associated with hunger and chronic stress. These changes include stereotypic behaviour and hyper activity, an increase in plasma corticosteronee level and heterophil to lymphocyte ratio and an increase in feed intake motivation (Gross and Siegel, 1983; Hocking et al., 1993; 1996; Savory et al., 1993; 1996; De Jong et al., 2002; 2003). Furthermore, a high degree of feed intake restriction is assumed to impair uniformity of broiler breeder live weight, egg weight and live weight of offspring (Zuidhof et al., 1995; Applegate, 2002). This might be due to an increased competition for feed when feed intake levels are restricted. A high uniformity in live weights of parent stock facilitates the adjustment of feed allowance on flock live weight development. It might also increase uniformity in offspring live weight, which is demanded and rewarded by slaughterhouses.

Because of the negative correlation between growth rate and reproductive performance, an increased feed allowance in order to improve broiler breeder welfare may have negative effects on hatching egg production. Since a decreased hatching egg production has major economic consequences for broiler meat production, other ways to improve broiler breeder welfare without negative effects on reproductive performance have to be considered. From a nutritional point of view, maintaining nutrient intake with increased feed intake levels by feeding low density diets might give an improvement of broiler breeder welfare without associated negative effect on the number of hatching eggs. Zuidhof et al. (1995) found a reduction in heterophil to lymphocyte ratio, an increased feed consumption time and a reduction in stereotypic behaviour without negative effects on performance when diets diluted with 15 or 30 % of oat hulls were given to broiler breeders. Moreover, they observed an increased uniformity in live weights of broiler breeders.

Low density diets: a pilot study

Mainly on the basis of the work of Zuidhof et al. (1995), a pilot study was started with Cobb 500 broiler breeders to evaluate effects of low-density diets on uniformity of broiler breeders and their offspring. Furthermore, some additional measurements were performed that might indicate changed bird welfare. In the pilot study, diets with three different nutrients were tested during the rearing and laying period. The control group included normal density diets with an AME content of 10.88 MJ/kg during the rearing period and an AME content of 11.72 MJ/kg during the laying period. In two other groups, the AME content of the feed was reduced with 1.26 MJ/kg and 2.51 MJ/kg respectively during both the rearing and the laying period. Each group included six replicates of 70 female birds and one replicate of 56 male birds each during the rearing period and six replicates of 70 female and 7 male birds each during the laying period. The reduction of the AME content of the diets was obtained by inclusion of low-density feedstuffs such as palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal. The intake of first limiting nutrients was kept constant in all treatments by decreasing these nutrients in the diet with the same percentage as the AME content. Then, daily feed allowance was increased with the same percentage as the dietary AME content was decreased. In the pilot study, target feed allowances and live weights of the Cobb 500 management guide were followed.

During the rearing period of the pilot experiment, no differences in plasma corticosteronee levels were detected between dietary treatments. A significant reduction in heterophil to lymphocyte ratios was observed at 9 weeks of age when low-density diets were given (Figure 1). Feed consumption time during the laying period was dramatically increased with low-density diets, as is illustrated in Figure 2 for 30-week old birds. These changes might indicate some changes in broiler breeder welfare. Since no other indicators for improved broiler breeder welfare were measured in this study, conclusions about effects of low density diets on broiler breeder welfare were taken cautiously.

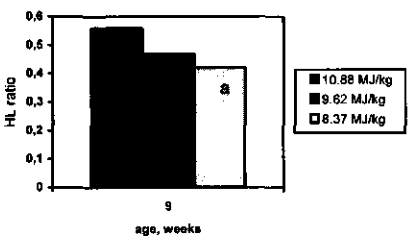

Figure 1. Effect of low-density diets on heterophil to lymphocyte (HL) ratio in 9-week old broiler breeders.

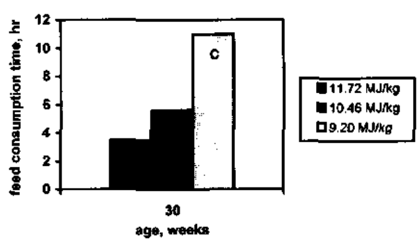

Figure 2. Effect of low-density diets on feed consumption time of broiler breeders of 30 weeks of age.

Since uniformity of broiler breeder and of offspring live weights were objectives of the pilot study, performance of offspring of broiler breeders given diets with different nutrient densities was determined as well. Per treatment, 4 replicates of male and 4 replicates of female birds with 170 birds per replicate were included in the offspring tests. Table 1 gives the offspring performance of 26- and 40-week old broiler breeders.

Table 1 Effect of low-density broiler breeder diets on offspring performance of 26- and 40-week old broiler breeders (numbers with different superscripts indicate significant differences at P≤0.05)

AME rearing diet, MJ/kg	10.88	9.62	8.37
AME laying diet, MJ/kg	11.72	10.46	9.20
Week 26			
Offspring live weight, day 14, g	405^{a}	416^{b}	422^{b}
Offspring live weight, day 30, g	1484^{a}	1505^{ab}	1528^{b}
Offspring live weight, day 39, g	2152	2183	2179
Offspring mortality, day 0-39, %	11.9^{c}	9.7^{b}	7.6^{a}
Week 40			
Offspring live weight, day 14, g	471^{a}	483^{b}	484^{b}
Offspring live weight, day 30, g	1647^{a}	1686^{b}	1688^{b}
Offspring live weight, day 39, g	2338	2361	2338
Offspring mortality, day 0-39, %	6.8^{b}	4.6^{a}	3.6^{a}

The results in Table 1 show that feeding low-density diets during the rearing and laying period increased offspring live weight at 14 and 30 days of age at both breeder ages. Differences in live weight at these ages followed differences in egg weight between treatments (data not shown). No significant differences in final live weight were observed. In broiler chickens of both 26- and 40-week old broiler breeders, a significant reduction in mortality rate was found when parents were fed low-density diets. The results of the pilot experiment indicate that broiler breeder diets can affect offspring performance and mortality.

Scope of the study

On the basis of the above mentioned pilot study and results of Zuidhof et al. (1995), it was questioned whether low-density diets could improve broiler breeder welfare. The pilot study had included only a few measurements to describe welfare and there was a need for a more detailed description of bird welfare to clarify effects of low-density diets on hunger and chronic stress in broiler breeders. Furthermore, there was no explanation for the observed effects of low-density diets on initial offspring growth and offspring mortality. Therefore, a second study with low-density broiler breeder diets was performed. The results of this second study are given in this thesis. The objectives of the study were:

- To investigate the effect of low-density diets on broiler breeder development during the rearing period in particular. Special attention was given to reproductive tract development.
- To study effects of low-density diets on bird behaviour, stress physiology and feed intake motivation.
- To determine effects of low-density diets on egg weight, egg composition and embryonic development.
- To relate changes in egg weight, egg composition and embryonic development to changes in offspring performance and mortality.
- To relate changes in offspring performance and mortality to changes in hunger feeling and chronic stress in parents.
- To investigate to what extend observed differences are related to the composition of low-density diets and the period these diets are applied.

Outline of the thesis

This thesis describes the results of a broiler breeder experiment that was performed during the entire rearing and laying period and experiments performed with their offspring. Chapter 2 reviews the effect of diet composition and feed intake on reproductive performance and broiler breeder welfare. Moreover, indications for effects of broiler breeder diets on offspring performance and offspring mortality are given.

Chapter 3 focuses on the effect of low-density diets and the composition of these diets on behaviour, stress physiology and feed intake motivation of broiler breeders during the rearing and laying period. Changes in plasma glucose and NEFA as indicators for nutritional status of birds are given in this chapter, as effects on feed intake motivation of the tested diets.

Effects of rearing diets with different nutrient densities and different feedstuff compositions on broiler breeder and reproductive tract development are described in Chapter 4. Chapter 4 also reports results of a digestibility experiment with low-density diets and relates differences in broiler breeder development to differences in nutrient digestibility and utilization of digested nutrients.

In Chapter 5, effects of low-density diets and composition of these diets on laying performance are presented. This chapter also describes the effect of low-density diets on egg composition and embryonic development at 29 and 41 weeks of breeder age. Chapter 6 gives performance and mortality rate data of broiler chickens of 29-, 41- en 60-week old broiler breeders fed diets with different densities and feedstuff compositions. Effect of these diets on humoral immune response is also given in this chapter. Effects of both broiler chicken performance and humoral immunity are related to egg weight and egg composition in chapter 6. The results described in the chapters 3, 4, 5 and 6 are discussed and evaluated in the General Discussion (Chapter 7). Results are compared with literature data and explanations for observed effects are given in terms of performed measurements and analyses.

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Chapter 2

Impact of broiler breeder nutrition on reproduction, offspring performance and bird welfare

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Abstract

Since ad libitum feed intake and a high growth rate in broiler breeders have a negative effect on reproductive performance, feed intake is restricted to improve this. However, there are indications that current levels of feed intake restriction can give hunger and chronic stress. On the basis of literature data, possibilities to increase feed intake without negative effect on reproductive performance are limited. However, there are indications that an increased dietary fibre content can increase satiety in broiler breeders, which might reduce hunger and chronic stress without negative effects on reproductive performance. There seem to be almost no possibilities to increase satiety in broiler breeders by changing dietary crude protein, amino acid, crude fat and starch levels. In this literature review, possibilities to improve reproductive performance and to reduce hunger and chronic stress in broiler breeders are given.

The occurrence of chronic stress might affect offspring performance due to negative effects of increased corticosteronee level in breeders. Also an increased variability in egg weight and egg composition might have an effect on offspring performance, particularly when breeders come into lay. On the basis of literature data, it can by hypothesized that an increased egg size and an increased amount of egg white and yolk can improve offspring performance. Possibilities to increase egg size and the amount of nutrients in eggs by changed compositions of broiler breeder diets are given. A limited number of experiments indicate that these changes can improve offspring performance.

Introduction

Growth rate of broiler chickens is an important economic parameter for broiler producers. A higher growth rate results in a higher live weight at a fixed age or in more production cycles per year when birds are slaughtered at a fixed live weight. To ensure a high live weight gain, growth rate is an essential selection criterion in broiler chicken breeding. Selection on growth rate, but also on feed intake, resulted in a clear increase in growth rate over the years (Havenstein et al., 1994).

Selection on increased live weight gain in broiler chickens however has a number of associated negative effects. Due to the negative genetic correlation between growth rate and reproductive performance, the number of hatching eggs has decreased over the years (Katanbaf, 1986; Hocking et al., 1987; 1994; 1996; Decuypere et al., 1999). In order to counteract this effect, restriction of feed intake has been successfully applied during the rearing and laying periods (Katanbaf et al., 1986; Bruggeman et al., 1999). However, current feed restriction levels are associated with hunger and chronic stress, particularly during the rearing period (Savory and Kostal, 1996; De Jong et al., 2002; 2003). Moreover, selection for a higher growth rate and impaired reproductive performance are also associated with an increased

variation in egg composition and an impaired performance of offspring of young broiler breeders (McNaughton et al., 1978; Applegate, 2002).
In order to counteract the negative effects that are associated with selection on an increased growth rate, different measures can be considered in terms of genetic selection, management and dietary composition. This paper will focus on the role of nutrition on broiler breeder reproduction, offspring performance and broiler breeder welfare. Figure 1 shows some possible relationships between broiler breeder nutrition during the rearing and laying periods and performance of offspring. These relationships will be discussed in this review.

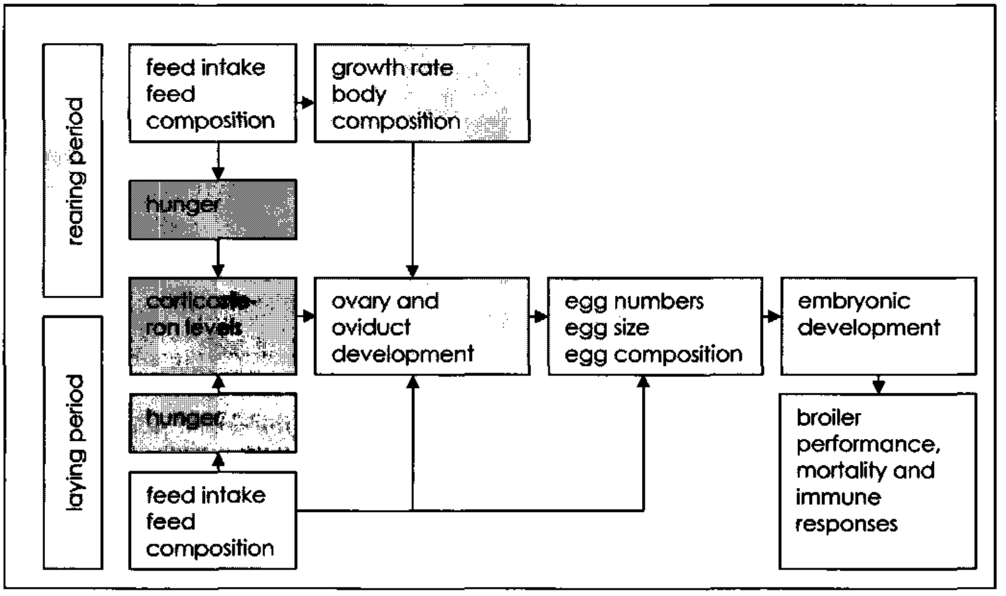

Figure 1. Possible effects of broiler breeder nutrition on hunger, stress, and reproductive and offspring performance.

Reproductive performance

When breeders are given unlimited access to feed, a high growth and fat deposition rate is associated with an impaired rate of lay and fertility rate (Katanbaf et al., 1986; Hocking et al., 1994; Decuypere et al., 1999; Applegate, 2002). Selection for increased body weight gain in broiler breeders is accompanied by increased ovulation rates in parent stock due to the simultaneous development of more than one ovarian yellow follicle (multiple ovulation; Hocking et al., 1989; 1987; Hocking, 1996). This results in an increase in egg shell abnormalities, more double yolked eggs and an increase in the number of yolks lost in the abdominal cavity (Nestor, 1985; Yu et al., 1992; Hocking, 1996; Hocking and Robertson, 2000). On the basis of many experiments, it appears that both the process of onset of lay and the processes involved in maintaining egg production have been influenced by selection on growth rate in broiler breeders (Hocking et al., 1989; 1994; 2002; Bruggeman, 1998; Renema et al., 1999).

Onset of lay is mainly regulated by the secretion of the gonadotrophins LH and FSH from the pituitary gland and gonadotrophin releasing hormones (GnRH) from the hypothalamus during aging of juvenile breeders (Etches, 1996; Bruggeman, 1998). Nutrient intake levels during the rearing period have an effect on the onset of sexual maturity (Lilburn and Nestor, 1993; Melnychuk et al., 1997; Renema et al., 1998; 1999). According to these authors, the development of ovary and ovarian hormones is stimulated by ad libitum feeding due to an earlier rise in levels of hormones like LH that are involved in the process of puberty. Oviduct development follows ovarian development on the basis of hormones released from that (Lilburn and Nestor, 1993; Melnychuk et al., 1997, Bruggeman, 1998; Renema et al., 1998). Negative effects of selection for an increased growth rate on ovary function have been associated with (changes in) insulin like growth factors and bone morphogenetic proteins (Ui et al., 1989; Monget et al., 1993; Onagbesan et al., 1995).
However, it is not clear yet how feeding levels affect reproductive hormone production from pituitary gland, hypothalamus and ovary. Katanbaf et al. (1989), Etches (1996) and Bruggeman (1998) suggested that factors associated with nutrient intake levels, age, body composition and ovarian development may be involved in this. Soller et al. (1984) and Bornstein et al. (1984) related onset of lay to body composition, while Yu et al. (1992) suggested that feed intake and growth rate were more important for the age at onset of lay. Both a minimum lean body weight and fat content seem to be required for onset of lay (Bornstein et al., 1984). Bruggeman et al. (1998) found that time and duration of feed restriction during the rearing period influenced reproductive performance. The highest egg production was obtained in groups that were restricted in the period from 7 to 15 weeks of age. This indicates that changes in nutrient intake in certain phases of the rearing period are particularly important for changes in reproductive hormones that regulate onset and maintenance of laying. In an extensive study in laying hens, Kwakkel et al. (1991; 1995) concluded that egg performance was affected by both phase and method of feed restriction during rearing.

During the laying period, the process of maintaining egg production mainly depends on the circadian rhythm that restricts LH release for ovulation to an 8 hour period of the day (Etches, 1984). Bruggeman et al. (1999) reported a higher plasma LH concentration and a higher LH/FSH ratio when birds were fed restrictedly compared with ad libitum fed birds. Bruggeman (1998) and Renema et al. (1999) related an increased LH/FSH ratio in restricted fed breeders with an increased sensitivity of the pituitary gland to feedback from hormones released from the ovary. This could result in a higher release of LH and in a higher egg production in restricted fed broiler breeders (Bruggeman, 1998). The higher LH/FSH ratio that was observed by

Bruggeman et al. (1999) and Renema et al. (1999), can also be involved in a reduction of the number of yellow follicles at the beginning of the laying period when feed intake is restricted (Hocking, 1993; 1996). The development of yellow follicles is affected by growth factors like IGF's (Hocking, 1992; Onagbesan and Peddie, 1995). This might explain the relation between growth rate and ovarian function (Bruggeman, 1998).

Egg size and composition

Applegate (2002) observed that variability in early egg production might be associated with changes in egg composition. This might be related to difference in carry over of digested nutrients to the egg. The changes and differences in egg composition might influence embryonic development, since nutrients in eggs are the only substrate for embryonic development (Romanoff, 1967; Applegate, 2002). Embryos from young broiler breeders develop more slowly than embryos from older breeders (Shanawany, 1984; Yannakopoulos and Tserveni-Gousi, 1987; Applegate and Lilburn, 1996; 1999; Christensen et al., 1996). This seems to be related to a larger proportional increase in yolk weight in eggs from older hens (Etches, 1996). Noble et al. (1986), Yaffei and Noble (1990) and Vajda et al. (1994) suggested that problems with embryonic development in eggs from young broiler breeders are due to an inefficient mobilization and use of yolk lipids. Konarzewski et al. (1989; 1990) and Ricklefs et al. (1998) regarded intestinal development is a main constraint for early post-hatch growth. Further indications for this were given by Applegate and Lilburn (1999) and Applegate et al. (1999), who found longer villi and better enterocyte migration in embryos from 48 week-old hens during the last stage of incubation compared with embryos from younger hens. Scavo et al. (1989) suggested that changes in insulin and IGF-I levels in young and older broiler breeders could be associated with differences offspring development. De Pablo et al. (1990) demonstrated that both insulin and IGF-I can have significant effects on early embryonic development. As with effects of IGF on reproductive performance, the findings of Scavo et al. (1989), and De Pablo et al. (1990) suggest that higher growth rates with increased IGF levels can affect embryonic development.

Due to the possible effects of egg composition on embryonic development, Applegate (2002) suggested that maximization of both egg and yolk size may minimize peaks in early mortality of offspring. This suggests that dietary factors, that increase egg size or change egg composition towards a higher yolk to egg white ratio, may affect offspring performance positively and reduce mortality. However, effects of dietary factors on egg size and composition and subsequent embryonic development and offspring performance have hardly been studied. Effects of diet composition on egg size and composition and possible effects on offspring performance are summarized in the next sections.

Energy intake and energy source

According to Gardner and Young (1972), dietary energy level has no effect on egg weight and egg composition. However, an increase in dietary fat level can increase egg weight (Whitehead et al., 1991; 1993). Whitehead et al. (1991) observed an increase in the percentage of egg white with increased dietary fat level in young laying hens. Effects of fat on egg weight are dependent on dietary fat composition; corn oil gives a significant increase in egg weight, whereas the same percentage of fish oil gives a significant reduction in egg weight compared with the same amount of lard (Whitehead et al., 1993; Whitehead, 1995). The inclusion of fish oil in the diet gives a significant reduction in yolk to egg white ratio (Whitehead et al., 1993). Dietary fat composition also affects yolk fat composition, since most fatty acids are deposited in the egg without transformation (Huyghebaert, 1985; Ahn et al., 1995; Cherian et al., 1996; Van Elswyk, 1997; Yannakopolous et al., 1999).

Although dietary fat level and fat composition seem to influence antibody responses (Craig-Schmidt et al., 1987; Fritsche et al., 1991; Friedman and Sklan, 1995; Parmentier et al., 1997), no clear and consistent effect of fatty acid content in parent stock diets on offspring immune responses and mortality have been reported (Peebles et al., 1998; 1999; Halle, 1999). Vilchez et al. (1991) observed an increase in embryonic mortality when quail parent stock diets contained linoleic acid instead of palmitic acid or stearic acid.

Triyuwanta et al. (1992a) observed a decreased egg weight when broiler breeders were fed more restrictedly than advised by the breeding company during the rearing period. This decrease in egg weight gave a reduction in day-old chicken weight and in 40 d body weight of the offspring. The findings of Triyuwanta et al. (1992a) indicate that changes during the rearing period can affect offspring performance. Fattori et al. (1990; 1993) observed a decrease in rate of lay when broiler breeder feeding levels were below breeder company recommendations. This might suggest a relationship between laying and offspring performance.

Protein and amino acids

Butts and Cunningham (1972) and Gardner and Young (1972) observed an significant increase in egg weight, percentage of egg yolk and protein content of yolk and egg white when dietary crude protein levels were increased from 120 to 180 g/kg. The composition of egg white was not changed with higher dietary protein levels, indicating that the amount of egg albumin was increased as well (Butts and Cunningham, 1972). This might result in a higher amount of IgM in eggs when the amount of egg white is increased. These antibodies can be absorbed by the intestinal tract of the embryo during incubation and might stimulate offspring immunity (Tizard, 1982; Griffin, 1989). Spratt and Leeson (1987) observed an increase in the percentage of egg white with increased dietary crude protein levels. They found that day-old chicken weight was affected by the protein to energy ratio in the broiler breeder diet. The only indication that changes in egg weight and egg composition with increasing dietary protein levels can affect offspring performance, was given by Lopez and Leeson (1994). They observed a decreased mortality rate in male broiler chickens when protein levels in parent diets were increased from 9 to 15 %.This reduction was not observed in female broiler chickens.

An increase in dietary methionine level can result in a higher egg weight, a higher protein content in egg white and yolk (Shafer et al., 1996), a higher proportion of egg white (Hussein and Harms, 1994) and a higher content of yolk phospholipids (Tsiagbe et al., 1988). However, Shafer et al. (1996) did not observe changes in the percentage of egg white and yolk with increasing dietary methionine levels. Al Bustany and Elwinger (1987) found an increase in egg weight and a higher dry matter content in egg yolk with increasing dietary lysine levels. No effects on percentage egg white and yolk were observed. Hussein and Harms (1994) observed an increase in egg weight and percentage of egg white with an increased dietary tryptophane level.

Vitamins and minerals

Hossain et al. (1998) et al. did not observe a reduction in offspring mortality when vitamin E levels were increased in broiler breeders diets, but the injection of vitamin E in egg resulted in a significant reduction in mortality of broiler chickens. Both the increase of vitamine E levels in broiler breeder diets and the administration of vitamin E directly into hatching eggs increased NCD antibody titers in offspring significantly. Naber (1993) has shown that higher dietary vitamin levels give higher vitamin levels in eggs. Besides, Nemecz and Mennear (1995) found changes in phospholipid composition in yolk with increased dietary vitamin E levels. This was not observed by Shafey et al. (1996). Tsiagbe et al. (1988) showed that increased dietary choline levels can increase yolk phospholipid content and composition.

Increased dietary mineral levels can also result in higher levels in eggs. This has been demonstrated for selenium (Davis and Fear, 1996), iodine (Kroupova et al., 1999) and iron (ShengFeng et al., 1999). For other minerals, indirect indications of transfer from diets to eggs have been obtained. Monsey et al. (1977) and Balnave and Scott (1985) found changes in egg white characteristics with increased dietary magnesium and copper levels. Flinchum et al. (1989) found an improved survival rate of chickens challenged with E. coli when zinc levels in parent stock diets were increased. An improved immunity of offspring was found by Kidd et al. (1993) when parents were given diets with increased zinc and manganese levels. Triyuwanta et al. (1992) demonstrated that increased phosphorus levels in parent stock diets increased bone strength in offspring.

Summarizing, feed intake, growth rate and reproductive performance are closely linked to each other in broiler breeders. An increased feed intake during the rearing period compared with current feed intakes gives a reduction in the number of hatching eggs. However, this impaired reproductive performance is not observed when feed intake is increased during the first and last third part of the rearing period. Higher feed intake levels might reduce chronic stress and hunger in broiler breeders and might have an effect on offspring due to reduced corticosteronee levels and an improved immune status.

In literature, there are only a few indications that broiler breeder diets can affect offspring performance, immune status and mortality. Most indications are based on the observation that egg composition can affect embryonic development en offspring growth. Changes in egg composition, that are due to changes in dietary composition, might therefore also affect embryonic development and offspring performance.

Hunger and chronic stress

According to Savory and Kostal (1996) and De Jong et al. (2002), the level of feed restriction of broiler breeders during the rearing period can be up to one-third of the ad libitium feed intake. During the laying period, the severity of restriction is smaller (De Jong et al., 2002). There are several indications for impaired broiler breeder welfare at current levels of feed restriction. Changes in behaviour, like an increase in stereotypic behaviour and hyperactivity, increases in plasma corticosteronee levels, heterophil to lymphocyte ratios and in feed intake motivation have been reported (Gross and Siegel, 1983; Savory et al., 1992; 1993; 1996; Savory and Moros, 1993; Hocking et al., 1993; 1996; Savory and Kostal, 1994; 1996; Savory and Mann, 1997; De Jong et al., 2002; 2003). These changes seem to be related to hunger feeling and frustration and may be associated with chronic stress.

According to Etches et al. (1984), Cain and Lien (1985), Greenberg and Wingfield (1987) and Sorenson (1997), increased levels of corticosteronee can be associated with decreased concentrations of reproductive hormones as LH. Silverin (1998) suggested that stress, resulting in increased corticosteronee and ACTH levels, can have a direct negative effect on reproductive performance. This indicates that feed restriction also might exert an effect on reproductive performance by changes in stress hormone levels.

Increased levels of corticosteronee at higher levels of feed restriction might also have an effect on egg composition and offspring performance. According to Tizard (1992) and Griffin (1989), corticosteronee can be immunosuppressive in different ways. In the case increased corticosteronee levels decrease antibody production in broiler breeders, a lower amount of maternal antibodies may be transferred to eggs (Knorr, 1991). This might impair both serum and antibody levels in offspring, since IgG is deposited in yolk and present in the circulation of the embryo by the absorption of yolk, while IgM is deposited in egg white and is integrated in intestinal tissue (Tizard, 1982; Knorr, 1991).

Feed intake motivation

The signs of stress and frustration, that are observed when broiler breeders are fed restrictedly, indicate that birds are willing to consume more food than they are offered (Ehlhardt et al., 1997; 2000; De Jong et al., 2002; 2003). Feed intake and feed intake motivation are the result of a complex of different mechanisms, which involve regulation by the central nervous system, hormones and nutrient levels in blood and tissues (Boorman and Freeman, 1979; Forbes, 1988; 1995; 1999; Blundell and Halford, 1994; Denbow, 1994a&b; Kuenzel, 1994; Strubbe, 1994). Bokkers and Koene (2003) distinguished pre prandial and post prandial factors in feed intake motivation. They associated pre prandial factors mainly with the satiety mechanism and postprandial factors with the hunger mechanism. According to Forbes (1999), three main factors can be indicated in the regulation of feed intake. These factors include *oropharyngeal factors, gastrointestinal factors and postabsorptive factors.*

Oropharyngeal factors

The smell and taste of feed or the presentation of feed itself can induce feed intake. This can be due to learned associations between the sight of feed and the nutritional properties of the feed (Forbes, 1988; 1995; Picard et al., 1997). Palatability of diets does not play an important role in poultry, since the number of taste receptors is low compared with other species (Sturkie, 1976). Particle size of diets or dietary components seem to be more important in feed intake than palatability (Portella et al., 1988a; b; Nir et al., 1990; Picard, 2000).

Gastrointestinal factors

The motivation to consume feed can be induced by the emptying of the digestive tract. Information from mechanoreceptors in the wall of the crop, gizzard and intestines and from specific chemoreceptors in the intestinal wall is transferred to the central nervous system (Mei, 1985; Greenberg et al., 1989; Forbes and Barrio, 1992). The emptying of the digestive tract is mediated by gastro-intestinal hormones, which are produced when feed or specific nutrients are present in the intestinal tract. The release of these hormones reduces feed intake (Baile et al., 1986; Morley, 1987; Moffet et al., 1993; Kuenzel, 1994) and slows down feed passage rate (Cuche and Malbert, 1999; Cuche et al., 2000).
Savory (1981) suggested that maximum feed intake capacity in broiler chickens and their parents is more determining feed intake than nutrient levels in blood after feed consumption. Burkhart et al. (1983) concluded that selection for an increased growth rate in broiler chickens has resulted in a reduction in satiety due to nutrient levels in blood and has lead to feed intake levels at near-capacity of the digestive tract. This was also concluded by Bokkers and Koene (2002) and by Barbato (1994) on the basis of work of Nir et al. (1978) and Barbato et al. (1984). Chickens selected for low live

weight gain showed feed intake levels that were far below intestinal tract capacity (Barbato, 1994). Bokkers and Koene (2003) indicated that eating behaviour of broiler chickens is controlled more by physical satiety mechanisms than by hunger mechanisms. Their findings suggest also that broiler chickens and their parents eat to their maximum capacity. This indicates that diets that increase gastrointestinal filling or decrease feed passage rate might increase satiety.

Post absorptive factors

A reduction in the amount of feed given results in changes in nutrient levels in blood. De Jong et al. (2003) have shown that a reduction in feed intake level in broiler breeders results in a sharp increase in the ratio between glucose and NEFA in blood plasma. This ratio indicates a change in nutritional status. The glucose concentration did not significantly differ between ad libitum and restricted fed birds. Glucose plays a central role in the regulation of feed intake and blood plasma levels are kept constant (Oomura, 1983; Campfield et al., 1985; Grill, 1986; Ritter and Edwards, 1986; Forbes, 1999). This is related to the role of glucose in energy metabolism, the fact that glucose levels fluctuate with meals and that feed consumption is terminated when glucose is given intravenously (Forbes 1988; 1995).
Besides changes in nutrient levels in the blood, changes in levels in depots in liver and other body tissues might signalize that feed has to be consumed to maintain these levels (Forbes, 1995). A reduction in feed intake can affect the amount of fat that is deposited in broiler breeders (Bornstein et al., 1984; Soller et al., 1984). A reduced fat deposition or mobilization from depot fat can give signals that stores have to be refilled. These signals can originate from changes in deposition or mobilization itself, from metabolites produced from mobilized stores or can be mediated by hormones like leptin (Anderson and Li, 1987; Forbes, 1988; Denbow, 1994a).

Physical satiety

Although infusions in blood with different nutrients (glucose, amino acids, fatty acids) have shown to reduce feed intake (Forbes 1988; 1995), there are almost no indications that digestible nutrient levels in iso energetic diets with balanced amino acid profiles can affect satiety. Mateos et al. (1982) observed a reduced feed passage rate on increasing dietary fat levels. Han and Baker (1993; 1994) and Fatufa et al. (2004) observed a reduced feed intake of broiler chickens at low protein diets. However, this does not seem to increase satiety, since low dietary protein levels can increase the incidence of abnormal behaviour as aggressive feather pecking (Ambrosen and Petersen, 1997; Elwinger et al., 2002). Unbalanced diets have shown to decrease satiety, as birds may choose different ingredients in order to finally ingest a more balanced menu (Forbes and Shariatmadari, 1994).
Since broilers seem to consume to their maximum intake capacity and that physical

capacity seems to maximize feed intake (Bokkers and Koene, 2003), an increase in the contents of the gastrointestinal tract might increase satiety and might reduce hunger feeling. The increase in gut content might be related to a higher bulk capacity of the diet or to changes in transit time through the intestinal tract. Forbes (1999) discussed effects of diet composition on feed intake in terms of minimal total discomfort. This idea of describing feed intake regulation means that also dietary factors, that increase abnormal or redirected behaviour, can give indications for changes in satiety.

Studies performed with restricted fed sows indicate that feeding fibrous diets reduce hunger feeling and frustration as measured by reduced stereotypic behaviour and reduced feed intake motivation (Robert et al., 1993; 1997; Brouns et al., 1994; Bergeron et al., 2000; Meunier-Salaun et al., 2001; De Leeuw, 2004).

In studies with broiler breeders during the rearing period, Savory et al. (1996) and Savory and Lariviere (2000) observed no reduction of stereotypic behaviour, plasma corticosterone concentration and heterophil to lymphocyte ratios on fibre rich diets, indicating that bird welfare was not improved. Van der Lee et al. (2001) found a reduction in abnormal behaviour on fibre rich diets in laying hens, which might indicate an increased satiety. Recently, Hocking et al. (2004) observed a decreased spot pecking on diets containing 5 % sugar beet pulp and 20 % oat hulls compared with a control diet. The highest heterophil to lymphocyte ratios were found in the low fibre control group and in the group with 5 % sugar beet pulp in the diet. Hocking et al. (2004) proposed that diets with sugar beet pulp could improve satiety and welfare due to a higher water content in the digestive tract.

In fibre rich diets and feedstuffs, a distinction should be made between soluble and insoluble fibres (Smits, 1996). Increased dietary insoluble fibre contents of different origins (cellulose, methylcellulose or rice hulls) gave an increased feed passage rate in broiler chickens and broiler breeders (Hennig and Jeroch, 1965; Savory, 1980; Alvares and Sanz, 1984; Leeson et al., 1991). Savory (1980), who reduced the energy content of quail diets with 40 % cellulose, found an increased feed intake, an increased feed consumption time and shorter intervals between meals. Based on these findings, Savory (1980) concluded that nutritional satiety is not substantially improved with diluted diets. However, Zuidhof et al. (1995) observed changes in behaviour and a decreased heterophil to lymphocyte ratio when broiler breeder diets were diluted with 15 or 30 % of oat hulls. Hartini et al. (2002) and Hetland and Choct (2003) found an increased feed consumption time and a reduced incidence of feather pecking on increased dietary levels of insoluble fibre, indicating an increased satiety. Hetland and Svihus (2001) and Svihus et al. (2002) demonstrated that coarse insoluble fibre fractions reduced passage rate of fine feed particles, which might also increase satiety.

In contrast to insoluble fibres, soluble fibres like carboxymethylcellulose and guar gum, gave a decrease in feed passage rate and feed intake (Van der Klis and Van

Voorst, 1993; Furuse and Mabayo, 1996). Diets with increased pectin levels as soluble fibre source decreased feed intake (Romruen et al., 1988; Drochner et al., 1990). Langhout (1998) noticed a lower feed intake on diets with highly methylated citrus pectin.

Van der Klis and Van Voorst (1993) and Smits (1997) related the reduction in feed intake to an increased digesta viscosity (Van der Klis and Van Voorst, 1993; Smits, 1997). In pigs, soluble fibres result in a delayed emptying of the stomach (Rainbird and Low, 1986a; b; Johansen et al., 1996). Based on experiments with different soluble fibres, a decreased feed passage rate can be associated with a decrease in feed intake. This might enhance nutritional satiety. Since Son et al. (2000) observed a decreased feed passage time in caecectomised broiler chickens compared with intact birds, fermentation products formed in the caeca with increased soluble fibre levels might play a role in feed passage rate and satiety.

It can be summarized that hunger and chronic stress in broiler breeders can be reduced with higher feed intake levels. However, this will have a negative effect on reproductive performance. There are almost no indications that changes in dietary crude protein, amino acids, crude fat and starch levels affect hunger and chronic stress in broiler breeders. Diet compositions that increase the amount of bulk and mean retention time in the gastrointestinal tract may reduce hunger and chronic stress. Increased levels of dietary fibre are the main dietary factor that seems to suited to reduce hunger in broiler breeders. However, this can depend on the type of fibre used in diets.

Conclusions

Feed intake, growth rate and reproductive performance in closely related to each other in broiler breeders. In order to increase the number of hatching eggs, feed intake has to be restricted, particularly during the rearing period. This implies that an increased feed intake compared with current practical restricted feed intakes will have a negative effect on reproductive performance. Therefore, this measure to reduce hunger and chronic stress in broiler breeders can not be applied in practice.

There is limited information about the effect of dietary composition on hunger and chronic stress. Diet compositions that increase bulk and/or reduce feed transit time in the gastrointestinal tract might have most perspective to reduce hunger and chronic stress in broiler breeders.

A reduction in chronic stress in broiler breeders might have an indirect effect on offspring performance due to an improved immune status of parents and an increased deposition of maternal antibodies in eggs due to this. Based on the observation that egg size, egg yolk to white ratio and offspring performance increase with broiler breeder age, changes in egg size and egg composition as a result of changes in dietary composition might therefore also have an effect on offspring performance. However, information about the effect of nutrient intake and chronic stress of broiler breeders on nutrient deposition in eggs and subsequent effects on embryonic development and offspring performance is scarce.

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Chapter 3

Do low density diets improve broiler breeder welfare during rearing and laying?

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Abstract

Low density diets may improve welfare of restricted fed broiler breeders by increasing feed intake time with less frustration of feed intake behaviour as a result. Moreover, low density diets may promote satiety through a more filled gastro-intestinal tract and thus feelings of hunger may be reduced. Broiler breeders were fed 4 different diets during the rearing and laying periods. Behavioural and physiological parameters were measured at different ages as indicators of hunger and frustration of the feeding motivation. A diet of 8.4 MJ/kg as compared with a standard diet of 10.9 MJ/kg extended feeding time and reduced stereotypic object pecking at 6 and 10 weeks of age. Furthermore, compensatory feed intake at 12 weeks of age was reduced. During lay, differences in behaviour were observed between the treatments that could be attributed to differences in feeding time. However, birds fed the diet with the lowest energy content, i.e. 9.2 MJ/kg had higher heterophil to lymphocyte (H/L) at 40 weeks of age compared with the other treatments, indicating that they experienced more stress during the laying period than the other treatments. This result could have been due to the very long feeding time of this treatment group during lay, which may be stressful. In conclusion, a low-density diet of 8.4 MJ/kg may reduce hunger and frustration in the first half of the rearing period. However, for substantial improvement of broiler breeder welfare during rearing, more extreme diet modifications are required.

Introduction

Due to the genetic selection for a high growth rate of progeny, broiler breeders have a high growth potential and need to be feed restricted to prevent health and reproduction problems at later age (Hocking et al., 1994). During rearing especially the daily ration is severely restricted and may be reduced to one-third of the intake of ad libitum fed birds of the same age or half of the intake of ad libitum fed birds of the same weight (Savory and Kostal, 1996; De Jong et al., 2002). The daily ration during the laying period varies between 70 and 100% of the intake of ad libitum fed birds of the same age (Zuidhof et al., 1995; Bruggeman et al., 1999).

During rearing, broiler breeders on restricted feeding show behaviours indicative of hunger and frustration of the feeding motivation, such as stereotypic (object) pecking, overdrinking, and pacing (Savory et al., 1992; Hocking et al., 1993; Savory and Maros, 1993; Hocking et al., 1996; Savory and Kostal, 1996; De Jong et al., 2002). Stereotypic object pecking has also been observed during laying (Zuidhof et al., 1995), suggesting that during lay the birds also seem to suffer from hunger and frustration. Operant feeding tests and measurements of compensatory feed intake show that broiler breeders on restricted feeding have a very high motivation to eat (Savory et al., 1993; De Jong et al., 2003). Moreover, increased plasma corticosteronee concentrations indicate that the practical restriction levels during rearing may induce chronic stress (Hocking et al., 1996; Savory and Mann, 1997; De Jong et al., 2002). It is therefore very likely that restricted feeding of broiler breeders prevents reproductive problems and health problems at the expense of increased hunger and frustration of the feeding motivation, thus deteriorating their welfare (Hocking et al., 1993; Savory and Maros, 1993; Savory et al., 1993; Savory and Kostal, 1994; Savory, 1995; Hocking et al., 1996; Savory and Kostal, 1996; Hocking et al., 2001; De Jong et al., 2002; Mench, 2002).

An alternative feeding method to improve broiler breeder welfare during rearing may be a low-density diet (Savory et al., 1993; Savory et al., 1996; Savory and Lariviere, 2000). This may extend the time spent eating and reduce the frustration of the feeding motivation. Moreover, low-density diets may fill gastro-intestinal tract, thus promoting feelings of satiety and reducing feelings of hunger (Whittaker et al., 1998; Whittaker et al., 1999). Studies with sows on restricted feeding indicate that increasing the fiber content of the diet reduced post feeding stereotypic behaviour and feeding motivation, which are indicators of hunger and frustration (Robert et al., 1993; Brouns et al., 1994; Bergeron et al., 2000; Meunier-Salaun et al., 2001). On the other hand, animals can still be metabolically hungry despite the filled gastrointestinal tract.

Results of previous studies using low-density diets to improve broiler breeder welfare have been contradictory. Diets with increased fiber contents have failed to improve broiler welfare as measured by stereotypic behaviour, plasma corticosteronee concentrations, heterophil to lymphocyte ratio (H/L) and responses in operant feeding tests (Savory et al., 1996; Savory and Lariviere, 2000). In contrast, Zuidhof et al. (Zuidhof et al., 1995) suggested that broiler breeder welfare during rearing improved after supplying feed with increased levels of dietary fiber based on measuring stereotypic behaviour and the H/L (Zuidhof et al., 1995). Recently, feeds diluted with sunflower seed meal, wheat bran, Lucerne, wheat gluten feed, and palm kernel meal appeared to improve broiler breeder egg production, flock uniformity, and performance of the broiler progeny and lowered H/L (H. Enting, 2003, Schothorst Feed Research, Lelystad, The Netherlands, personal communication) suggesting that the birds may experience less stress (Gross and Siegel, 1983) as compared with broiler breeders fed a standard diet. As these results are promising, the effects of these low-density diets on broiler breeder welfare and performance during rearing and in the laying period were studied in more detail. In the present paper we focussed on the effect of these different diets on broiler breeder welfare. Bird welfare was assessed using a wide range of behavioural and physiological parameters indicative of hunger and frustration of the feeding motivation, including stereotypic object pecking and activity level (Savory and Maros, 1993; Hocking et al., 1996; Savory and Kostal, 1996; De Jong et al., 2002), feeding motivation (De Jong et al., 2003), H/L (Gross and Siegel, 1983; Savory et al., 1996), plasma corticosteronee concentrations (Savory and Kostal, 1994; Hocking et al., 1996; De Jong et al., 2002; De Jong et al., 2003) and glucose-nonesterified fatty acid ratios (De Jong et al., 2003). The standard diet was diluted with sunflower seed meal, wheat bran, lucerne, wheat gluten feed, and palm kernel meal in 2 concentrations or with sugar beet pulp and oats.

Materials and methods

Birds and Housing

Birds were housed at 'De Schothorst' experimental farm, Lelystad, The Netherlands. We used a total of 24 pens with 90 female broiler breeders (Cobb 500, Putten, The Netherlands) per pen during rearing (day 1 to 24 weeks of age) and 70 female broiler breeders per pen during laying (25 to 60 weeks of age) in the experiment. Chicks arrived at the day of hatching. Cocks were reared elsewhere and introduced into the pens when the hens were 20 weeks of age. Six cocks were added per pen. Beak trimming was carried out at 4 days of age and for the cocks toes were clipped on day 1. A standard vaccination program was applied.

Birds were housed in two identical climate-controlled rooms (12 pens per room) in litter pens (4.5 x 3.0 m, wood shavings). Per pen, a heightened floor of 1.2 x 1.9 m with plastic slats was provided, and four laying nests (95 x 32 x 34 cm) were available to the hens from 20 weeks of age onward. Pens were separated by a wire mesh. Per pen, 5 automatic feed hoppers and 1 automatic drinking bowl was available. Feed was provided at 08.15 h. Water was provided from 07.45 h until 30 min after the troughs were empty for the treatment group with the longest feeding time. This means that water bowls were always empty from 10.15 h onward during rearing.

A standard temperature and light schedule was applied. Temperature was lowered from 32°C at day 1 to 20°C from 10 weeks of age onward. The photoperiod was shortened from 24 h at week 1 and 2 to 8 h from 3 weeks of age. From 18 weeks of age, the photoperiod was gradually increased from 10 to 16 h at 30 weeks of age. Lights (5 lux) were always switched on at 07.45 h. Treatments (see below) were randomly assigned to the pens and equally distributed over the rooms. In one room, an extra pen with 80 hens was present. These hens were fed ad libitum and used as a control in the feed intake motivation test (see below).

Treatments

Four different treatments (n=6 pens per treatment) were applied as shown in Tables 1 and 2. All birds received standard feed (treatment 1) of 10.9 MJ/kg ad libitum until 21 days of age. From this age birds were fed restricted rations (Table 1, 4-24 weeks;

Table 2, 25-60 weeks). The amount of feed provided was adjusted to meet a target body weight. Feed treatments 2 and 3 were diluted by palm kernel meal, wheat bran, Lucerne, and wheat gluten feed, and sun flower seed meal; feed treatment 4 was diluted by sugar beet pulp and oats. Birds were weighed every 3 weeks. If the weight differed more than 5% from the goal weight according to the Cobb schedule, the feeding schedule was adapted.

Behavioural Observations

At 6, 10, 13, 16, 20, 26, 30, 40 and 60 weeks of age, we scored the time until feed hoppers were empty per pen. In each room one person scored the time at which all feed hoppers in one pen were empty.
Behaviour of the birds was observed in the home pen at 6, 10, 16, 20, 26 and 40 weeks of age by scan sampling. Per pen, behaviour was simultaneously scored in the 2 rooms by two persons. The 2 observers were trained beforehand to ensure that behaviours were classified into the same categories. For each pen, behaviours of birds were scored by counting the number of birds in half of the pen engaged in different activities according to the ethogram (Table 3). This included half of the feed hoppers and half of the drinking bowl. Behaviour was observed around feeding between 07.45 - 11.45 h and between 12.15 - 15.45 h on 2 consecutive days. Pens were observed 15 times in total per age period. For the rearing period, we analyzed the behaviour during the observation sessions in which feed and water were no longer available (from 10.15 h onward). For these observations, stereotypic object pecking was defined as pecking at the empty feed hoppers, empty water bowls, and the pen or walls. In the laying period, feed and water were available much longer, and we thus could not analyze behaviour when feed and water were no longer available for all treatments. Therefore, pecking at the empty feeder, which could have occurred during the laying period for some treatments, could not be included in object pecking.

Blood Sampling; Glucose, Nonesterified Fatty Acid, and Corticosteronee Concentrations; and H/L

At 6, 10, 16, 20, 26 and 40 weeks of age, one day after the behavioural observations, blood was collected from the wing vein by venipuncture of 5 birds per pen between 10.00 - 12.30 h. Pens were selected in random order for blood sampling, and both rooms were sampled simultaneously. Hens were quietly approached and quickly picked up, and blood was sampled (2.5 mL) within 1.5 min after catching. To determine H/L, plasma glucose, and corticosteronee concentrations, blood was stored in heparinized tubes on ice. For determination of plasma nonesterified fatty acid (NEFA) concentrations, blood was stored in EDTA tubes on ice.

Table 1. Feed composition (%) and calculated contents (g/kg) of the different types of feed in the rearing period

	Weeks 4-6				Weeks 7-24			
AME, MJ/kg	10.9	9.6	8.4	9.6	10.9	9.6	8.4	9.6
Treatment group	1	2	3	4	1	2	3	4
Ingredient								
Oats				15.00				15.00
Rapeseed meal	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
Lucerne		1.44	2.88			1.47	2.93	
Corn	25.00	25.00	25.00	25.00	25.00	25.00	25.00	25.00
Corn gluten feed	10.00	10.00	10.00		10.00	10.00	10.00	
Palmkernel meal		5.00	10.00			5.00	10.00	
Sugarbeet pulp				15.00				15.00
Soyabean meal	13.74	1.79	1.83	16.59	10.12	5.06		14.39
Wheat	34.78	20.58	6.37	11.79	31.84	20.78	9.71	17.36
Wheat bran		6.25	12.50	3.62	10.00	11.25	12.50	5.41
Wheat gluten feed		5.00	10.00	2.37		5.00	10.00	
Sunflowerseed meal	4.34	8.42	12.50		1.48	6.99	12.50	
Sugar cane molasses	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Soyabean oil	1.52	1.01	0.50	1.17	0.65	0.33		0.51
Animal fat	0.66	0.33			2.63	1.32		
Chalk/limestone	1.25	1.11	0.97	0.83	0.93	0.77	0.61	0.49
Monocalcium phosphate	0.67	0.38	0.09	0.94	0.07	0.04		0.54
Premix, vitamins and minerals	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Premix, lysine+methionine	1.08	0.54		0.53	0.36	0.18		0.04
Premix, phytase	0.40	0.40	0.40	0.03	0.40	0.26	0.11	
Premix, lysine		0.43	0.85		0.24	0.39	0.53	
Premix, methionine	0.27			0.89				0.01
Premix, acid	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Salt	0.28	0.20	0.11	0.25	0.28	0.19	0.10	0.26
Total	100	100	100	100	100	100	100	100
Calculated contents, g/kg								
Moisture	126	122	118	121	127	123	119	124
Ash	56	57	59	59	48	51	53	51
Crude protein	174	170	165	167	157	158	158	157
Digestible lysine	8.4	7.4	6.4	7.4	6.7	5.9	5.2	5.9
Digestible methionine+cystine	7.1	6.3	5.5	6.5	5.7	5.5	5.3	5.0
Crude fat	44	42	41	38	57	46	36	31
Linoleic acid	18	16	14	16	16	14	12	13
Crude fiber	40	65	90	65	40	65	90	65
Calcium	8.9	8.3	7.7	8.3	6.5	6.2	5.8	6.2
Phosphorus	3.7	3.3	2.9	3.3	2.6	2.4	2.2	2.4
Retainable phosphorus	5.9	6.3	6.6	5.9	5.0	5.7	6.4	5.0
Sodium	1.6	1.4	1.2	1.4	1.6	1.4	1.2	1.4
Chlorine	3.2	3.0	2.7	2.6	3.0	2.7	2.5	2.4
Potassium	8.4	9.2	9.9	8.9	8.4	9.0	9.6	8.4

Blood samples were centrifuged at 3,000 rpm at 4°C within 1 hour after sampling. Plasma. (150 µL) was stored at 4°C in tubes containing 0.1% (wt/vol) sodium azide until analysis for corticosteronee concentrations. Corticosteronee concentrations were determined in unextracted, enzymatically pre-treated plasma as described earlier (De Jong et al., 2001). Two sets of 100 µl of plasma were stored at –20°C until analysis for glucose and NEFA concentrations. Glucose concentrations were determined spectrophotometrically using the hexokinase method (Gluco-quant Test, Roche, Mijdrecht, The Netherlands; De Jong et al., 2003). NEFA concentrations were spectrofotometrically determined using a standard test kit (Wako, Richmond, USA; De Jong et al., 2003). The H/L were determined in 50 µL of blood by using an automatic cell counter with specialized software for chicken blood (Cell-Dyn 3500, Abbott Diagnostics, Amstelveen, The Netherlands) as described earlier in detail (Post et al., 2003).

Feed Intake Motivation Test

At 10 weeks of age, 2 birds were randomly selected from each of the 24 pens and transported in pairs to the experimental farm of the Animal Sciences Group. Twelve birds fed ad libitum were randomly selected from the extra pen, divided into 6 pairs, and also transported to the experimental farm. All 60 birds were housed pair wise in pens (0.75 x 1.0 m) with wood shavings and fed according to the treatment schedule. Water was available ad libitum. Lighting schedule and environmental temperature were as on the 'Schothorst' experimental farm. Dietary treatments (described in Table 1) were randomly assigned to 6 blocks of pens. After 1 week the feed intake motivation test was started (78 days of age). All birds were fed ad libitum from the same point (08.00 h), and their feed intakes were measured daily. Birds were weighed every 2 days, and the (caloric) feed intake per kilogram of metabolic weight was determined by measuring feed intake during 22 days.

Statistical Analysis

A regression model was used to determine treatment effects on feeding rate. After inspection of diagnostic plots of residuals, we decided to analyze the behavioural variables with a logistic regression model (data expressed as percentages).

A regression model was also used to determine treatment effects on plasma corticosteronee concentrations, glucose/NEFA ratio, and H/L. All models comprised main effects for treatments, room, and interactions. However, no significant effects for room or interactions were found, and these results were therefore not mentioned in the text. Estimation was performed by maximum quasi-likelihood. Significance tests were based on approximate *F*-tests. Pair wise comparisons were derived from a normal approximation. Details can be found in a report by McCullagh and Nelder (1989). All calculations were performed with the GenStat statistical programming language (Committee Genstat, 2000).

Table 2. Feed contents (%) and calculated contents (g/kg) of the different types of feed in the laying period

	Week 25-30				Week 31-60			
AME, MJ/kg	11.7	10.5	9.2	10.5	11.7	10.5	9.2	10.5
Treatment group	1	2	3	4	1	2	3	4
Ingredient								
Oats				15.00				15.00
Rapeseed meal	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
Lucerne		1.27	2.53			2.00	4.00	
Corn	25.00	25.00	25.00	25.00	30.00	30.00	30.00	30.00
Corn gluten feed	10.00	6.12	2.24		10.00	5.00		
Palmkernel meal		6.25	12.50			7.50	15.00	
Sugarbeet pulp				15.00				12.50
Soyabean meal	11.45	5.73		13.04	7.78	3.89		10.27
Wheat	21.16	15.07	8.98	13.06	17.93	13.20	8.46	9.98
Wheat bran	10.00	11.25	12.50		10.00	7.83	5.65	1.06
Wheat gluten feed		5.00	10.00			6.66	10.00	
Sunflowerseed meal	2.42	7.91	13.39	2.69	2.88	5.00	10.44	4.57
Lupins							3.06	
Sugar cane molasses	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Soyabean oil	0.69	0.68	0.67	1.01	0.14	0.31	0.47	0.36
Animal fat	5.11	2.61	0.10	1.86	5.75	2.88		2.38
Chalk/limestone	6.72	5.83	4.94	5.53	8.13	7.04	5.94	6.85
Monocalcium phosphate	0.23	0.14	0.05	0.65	0.06	0.03		0.28
Premix, vitamins and minerals	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Premix, phytase	0.40	0.28	0.16		0.40	0.28	0.16	0.16
Premix, lysine	0.21	0.33	0.44		0.33	0.32	0.31	
Premix, methionine				0.56				
Premix, acid	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Salt	0.11	0.06		0.09	0.10	0.06	0.01	0.09
Total	100	100	100	100	100	100	100	100
Calculated contents, g/kg								
Moisture	115	114	113	113	113	111	110	113
Ash	109	103	96	103	120	111	103	111
Crude protein	153	151	148	148	139	141	143	140
Digestible lysine	6.0	5.4	4.7	5.4	5.4	4.8	4.3	4.8
Digestible methionine+cystine	5.5	5.4	5.3	5.6	5.1	5.1	5.0	5.0
Crude fat	80	62	43	52	82	62	42	52
Linoleic acid	18	16	14	16	16	15	13	15
Crude fiber	40	65	90	65	40	65	90	65
Calcium	30.0	26.8	23.6	26.8	6.0	5.8	5.6	6.3
Phosphorus	5.2	5.6	6.0	4.7	4.6	4.8	5.0	4.0
Retainable phosphorus	2.8	2.5	2.2	2.5	2.6	2.4	2.2	2.4
Sodium	1.6	1.4	1.2	1.4	1.6	1.4	1.2	1.4
Chlorine	2.6	2.6	2.5	2.2	3.0	2.7	2.5	2.4
Potassium	8.3	8.6	8.8	7.7	8.4	9.0	9.6	8.4

Table 3. Ethogram of the behavioural measurements

Behaviour	Description
Peck feeder	pecking at the (empty) feeder
Peck drinker	pecking at the drinker
Walking	walking, running without performing foraging, comfort behaviour or pecking
Standing	standing without performing foraging, comfort behaviour or pecking
Sitting	sitting without performing foraging, comfort behaviour or pecking
Foraging	pecking, scratching the litter
Comfort	all comfort behaviour like preening, auto pecking, nibbling, stroking, wing flapping, stretching
Peck object	pecking at parts of the cage or at the wall
Peck bird	all peckings at other birds

Results

Feeding Duration

The time until the feed hoppers were empty and the amount of feed provided per treatment group are listed in Table 4. A significant treatment effect was found for the time until the hoppers were empty at all ages (6 weeks, $F_{3,23}$=109; 10 weeks, $F_{3,23}$=16.97; 13 weeks, $F_{3,23}$=56.01; 16 weeks, $F_{3,23}$=90.99; 20 weeks, $F_{3,23}$=170.45; 26 weeks, $F_{3,23}$=86.25; 30 weeks, $F_{3,23}$=58.07; 40 weeks, $F_{3,23}$=113.22; 40 weeks, $F_{3,23}$=37.43; P<0.001 at all ages).

Behaviour

Figure 1 shows the percentage of birds that pecked at objects (pecking at the empty feeder, the empty drinker, and objects) at 6, 10, 16 and 20 weeks of age. Treatment effects were found at 6 ($F_{3,23}$=7.75, P<0.001) and 10 ($F_{3,23}$=4.82, P<0.05) weeks of age, but not at other ages. At 6 and 10 weeks of age, a treatment effect on the time spent sitting was found (Figure 2, $F_{3,23}$=9.67, P<0.01 at 6 weeks and $F_{3,23}$=5.04, P<0.01 at 10 weeks). At 6 weeks, a significant treatment effect on the time spent standing was found ($F_{3,23}$=7.62, P<0.05). Birds of treatment 1 and 4 spent less time standing then those of treatments 2 and 3 (P<0.05; mean % of observations for treatment 1: 9.2±1.5%; treatment 2: 14.5±2.8%; treatment 3: 13.9±1.7%; treatment 4: 10.0±1.3%). At 16 weeks, a treatment effect on the time spent walking was observed ($F_{3,23}$=4.64, P<0.05). Birds of treatment 4 spent less time walking as compared with birds of treatment 2 (P<0.05) and 3 (P<0.01) (mean % of observations for treatment 1: 6.2±0.2%; treatment 2: 7.5±0.6%; treatment 3: 7.8±1.1%; treatment 4: 4.9±0.1%). No differences in other behaviours were found during the rearing period (overall means of the rearing period: foraging 6.5±0.5%; comfort behaviour 8.9±0.4%; pecking other birds 0.9±0.1).

Table 4. Feeding duration (min; means± SEM of 6 pens per treatment) and the amount of feed provided in the rearing period

	6 weeks		10 weeks		13 weeks		16 weeks		20 weeks		26 weeks		30 weeks		40 weeks		60 weeks	
Treat-ment	Time	gr/bird	Time	gr/bird	Time	gr/bird	Time	gr/bird	Time	gr/bird	Time	gr/bird	Time	gr/bird	Time	gr/bird	Time	gr/bird
1	45±0^{a}	49	57±4^{a}	56	30±0^{ac}	56	27±1^{a}	56	28±1^{a}	88	105±5^{a}	145	306±9^{a}	168	140±7^{a}	158	128±10^{a}	148
2	75±3^{b}	55	75±4^{b}	63	36±1^{b}	63	31±1^{b}	63	53±2^{b}	99	212±15^{b}	162	441±8^{b}	188	247±6^{b}	178	247±10^{b}	168
3	115±3^{c}	64	102±5^{b}	73	56±2^{d}	56	49±0^{c}	76	68±3^{c}	114	392±8^{c}	184	585±9^{c}	213	415±16^{c}	205	265±12^{c}	188
4	60±0^{d}	55	107±3^{c}	63	33±2^{c}	63	25±1^{ab}	63	45±0^{d}	107	213±18^{b}	162	504±25^{d}	192	251±6^{b}	181	235±19^{b}	168

[a-d] Means within a column lacking a common superscript differ (*P*<0.05 at least).

Table 5. Plasma corticosteronee, glucose and NEFA concentrations (means of 12 birds per treatment group ± SEM) and the glucose/NEFA ratio at 6, 10 and 26 weeks of age

	Corticosteronee (ng/ml)			glucose (mM)			NEFA (mM)			glucose/NEFA		
Treat-ment	6	10	26	6	10	26	6	10	26	6	10	26
1	0.74±0.06^{a}	0.37±0.03^{a}	2.77±0.25^{a}	14.3±0.2^{a}	13.1±0.1^{a}	16.4±0.4^{ab}	0.19±0.005^{a}	0.12±0.004^{a}	0.31±0.01^{a}	77.3±2.5^{a}	109.0±4.6^{a}	57.5±2.2^{a}
2	0.88±0.11^{a}	0.44±0.03^{a}	3.17±0.19^{a}	14.5±0.2^{a}	13.2±0.2^{a}	16.5±0.3^{a}	0.17±0.005^{a}	0.10±0.003^{b}	0.27±0.01^{a}	87.9±2.5^{b}	136.0±5.8^{b}	60.9±2.1^{a}
3	1.01±0.08^{a}	0.48±0.04^{a}	2.91±0.25^{a}	15.0±0.2^{a}	13.3±0.1^{a}	15.5±0.2^{b}	0.18±0.004^{a}	0.10±0.004^{b}	0.21±0.01^{b}	81.9±1.8^{ab}	133.2±5.7^{b}	77.0±2.7^{b}
4	0.93±0.07^{a}	0.44±0.04^{a}	2.57±0.26^{a}	14.6±0.1^{a}	13.3±0.1^{a}	15.6±0.3^{ab}	0.16±0.003^{a}	0.11±0.003^{b}	0.29±0.02^{a}	89.5±2.0^{b}	128.0±4.1^{b}	61.2±3.2^{a}

[a,b] Means within a column lacking a common superscript differ (*P*<0.05 at least).

Figure 3 shows the proportion of birds performing the behaviours at 26 weeks and Figure 4 shows the proportion of birds performing the behaviours at 40 weeks of age. At 26 weeks, treatment effects were present for time spent pecking at the feeder ($F_{3,23}$=15.88, P<0.001), walking ($F_{3,23}$=12.76, P<0.001), sitting ($F_{3,23}$=3.39, P<0.05), foraging ($F_{3,23}$=9.40, P=0.01), comfort behaviour ($F_{3,23}$=13.43, P=0.01) and object pecking ($F_{3,23}$=2.96, P<0.05). At 40 weeks treatment effects were present for time spent pecking at the feeder ($F_{3,23}$=31, P<0.001), walking ($F_{3,23}$=37.46, P<0.001), sitting ($F_{3,23}$=11.52, P<0.001) and object pecking ($F_{3,23}$=16.17, P<0.001).

Physiological Parameters

Plasma corticosteronee, NEFA, and glucose concentrations were determined in samples at 6, 10 and 26 weeks of age, as the greatest differences in behaviour were found at these ages. No treatment effects were found for plasma corticosteronee concentrations at these ages (Table 5). At all ages these were treatment effects for the glucose/NEFA ratio (Table 5; 6 weeks, $F_{3,119}$=4.92; 10 weeks $F_{3,98}$=3.91; 26 weeks, $F_{3,95}$=12.00; P<0.001 at all ages). At 10 weeks differences were found in NEFA concentrations, and at 26 weeks of age differences were found for glucose as well as NEFA concentrations (Table 5).

Although there were no treatment effects for H/L at 6, 10, 16, 20 and 26 weeks of age (Table 6), a treatment effect was present at 40 weeks of age ($F_{3,116}$=3.38, P=0.01, Table 6).

Table 6. Heterophil to lymphocyte ratios (H/L; means of 12 birds per treatment ± SEM) in the rearing and laying periods

Treat-	Age (weeks)					
ment	6	10	16	20	26	40
1	2.84±0.33^{a}	1.55±0.21^{a}	1.37±0.20^{a}	0.99±0.10^{a}	1.01±0.10^{a}	1.11±0.13^{a}
2	2.15±0.33^{a}	1.33±0.17^{a}	1.44±0.19^{a}	1.25±0.21^{a}	1.17±0.07^{a}	1.07±0.10^{a}
3	2.43±0.32^{a}	1.22±0.17^{a}	1.34±0.17^{a}	0.92±0.10^{a}	1.08±0.09^{a}	1.60±0.17^{b}
4	1.89±0.24^{a}	1.67±0.24^{a}	1.59±0.20^{a}	1.11±0.16^{a}	1.08±0.10^{a}	1.41±0.09^{ab}

^{a,b} Means within a column lacking a common superscript differ significantly (P<0.01).

Feed Intake Motivation Test

Figure 5 shows the relative compensatory feed intake for all treatments and the group fed ad libitum. Because birds received feeds with different energy contents, birds fed low-density diets should have a greater intake to realize equal energy intake. Therefore, the relative compensatory feed intake is shown in calories. Analysis was performed for treatments 1 to 4; thus, the group fed ad libitum was not included. Before the start of the test at day 76, no significant treatment effects were found in relative feed intake. Treatment effects were found for the following days: 78, 80, 82, 84 ($F_{3,23}$=50.12, $F_{3,23}$=19.96, $F_{3,23}$=28.54, $F_{3,23}$=12.44 respectively, P<0.001), 86 ($F_{3,23}$=7.61, P=0.001), 88, 90 and 94 ($F_{3,23}$=3.80, $F_{3,23}$=4.17, $F_{3,23}$=3.97 respectively, P<0.05).

Discussion

Feeding Duration and Behaviour

Feeding low density diets resulted in a significantly prolonged intake of the feed. This prolonged intake was greatest for birds fed the most diluted diet (treatment 3, 8.4 MJ/kg) at 6, 10, 20, 26, 30 and 40 weeks of age. In the middle of the rearing period differences among treatments were much smaller, probably because the amount of feed provided at 13 and 16 weeks of age was very small as compared with bird weight at those ages. At those ages even the birds fed the most diluted diets ate their daily ration within 1 hour. As the relative amount of feed provided during the laying period largely increases as compared with the rearing period (Bruggeman et al., 1999), the feeding time during the laying period also largely increases. For treatment group 3, feeding time even increased to more than 10 h at 30 weeks.

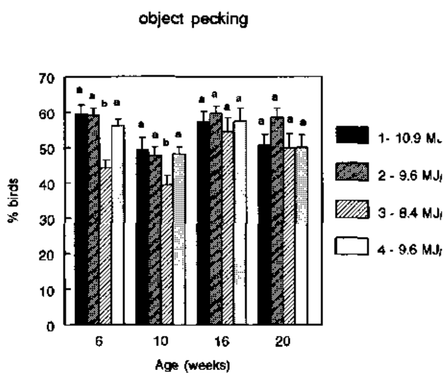

Figure 1. Percentage of birds showing object pecking during the rearing period (means of 6 pens per treatment ± SEM). [a,b] Different letters indicate significant differences among treatments (*P*<0.001 at 6 weeks of age, *P*<0.05 at 10 weeks of age).

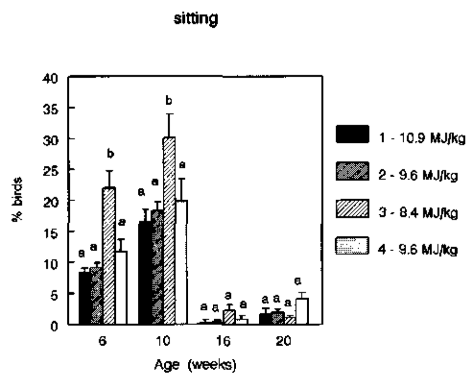

Figure 2. Percentage of birds sitting during the rearing period (means of 6 pens per treatment ± SEM). [a,b] Different letters indicate significant differences among treatments (*P*<0.01).

During the rearing period, differences in the time spent pecking at objects were only found at 6 and 10 weeks (i.e., ages at which the differences in feeding time among the treatments were greatest). The time spent pecking at objects was significantly lower for birds of treatment 3 but not for birds of treatments 2 and 4. Thus, it appears that a more pronounced and reduced energy content of the diet is necessary to decrease the time spent pecking at objects. The time spent pecking at objects is indicative of hunger and frustration of the feeding behaviour in broiler breeders (Savory and Maros, 1993; Hocking et al., 1996; Savory et al., 1996; Savory and Kostal, 1996). Thus, this result may indicate that there was a reduction in hunger or frustration of the feeding motivation in birds of treatment 3. However, it should be noticed that object pecking was still performed during a large part of the observed time (40 to60% of the observed time) for all treatments. This finding indicates that the reduction in hunger or frustration for birds of treatment 3 as compared with birds fed the standard diet was relatively small.

Besides the differences in object pecking, differences in the time spent sitting also were observed at 6 and 10 weeks. Birds of treatment group 3 spent more time sitting as compared with birds of the other treatments. Reduced activity may also indicate that hunger and frustration of the feeding motivation are reduced (Savory and Maros, 1993; Hocking et al., 1996; Savory et al., 1996). These data support the suggestion that birds of treatment group 3 experienced less hunger and frustration then those of other treatments.

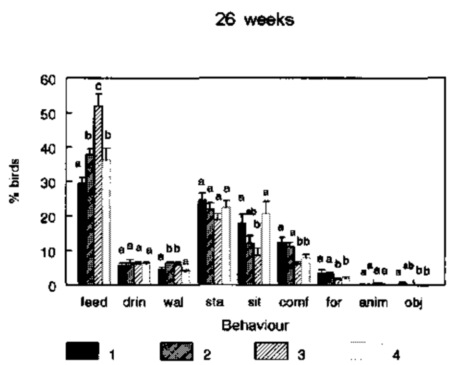

Figure 3. Percentages of birds observed behaviors at 26 weeks of age (means of 6 pens per treatment ± SEM). a-c Different letters indicate significant differences between the treatments (P<0.05 at least). Feed = pecking at the feeder; drink = pecking at the drinker; walk = walking; stand = standing; sit = sitting; comf = comfort behavior; for = foraging; anim = pecking at other animals; obj = object pecking.

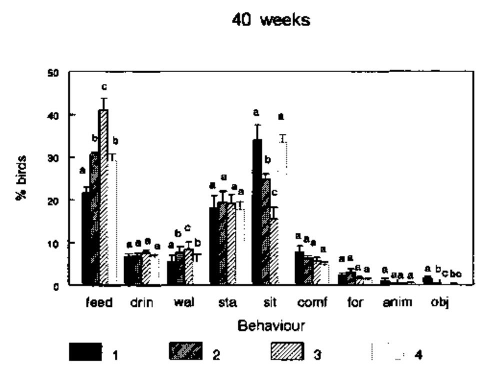

Figure 4. Percentages of birds showing the behaviors at 40 weeks of age (means of 6 pens per treatment ± SEM). a-c Different letters indicate significant differences among treatments (P<0.05 at least). Feed = pecking at the feeder; drink = pecking at the drinker; walk = walking; stand = standing; sit = sitting; comf = comfort behavior; for = foraging; anim = pecking at other animals; obj = object pecking

Differences in behaviour among treatments during the laying period most probably were to be caused by differences in feeding time. Birds of treatment group 3 spent more time on feeding and less time on other behavioural elements, such as sitting and foraging, and on comfort behaviour. Object pecking is almost absent during lay, indicating that frustration and hunger are almost absent (Savory and Maros, 1993; Hocking et al., 1996; Savory and Kostal, 1996), although we cannot exclude that some birds might have pecked at the empty feeder, as we could not analyze this separately during the laying period. This finding is in contrast to the observations of

Zuidhof et al. (1995), who reported that the time spent object pecking in the first half of the laying period is equal to that for the rearing period. As in the present experiment, behaviour was observed during the first half of the lighting period, and it might be possible that object pecking could be observed during the second half of the lighting period. However, this is unlikely as object pecking caused by hunger and frustration of the feeding motivation predominantly occurs in the hours after feeding (Savory and Kostal, 1996) and this period was included in our observations. No differences were found in behaviour between treatment group 2 and 4. A different feed composition, but the same energy content, did thus not have any effect on bird behaviour.

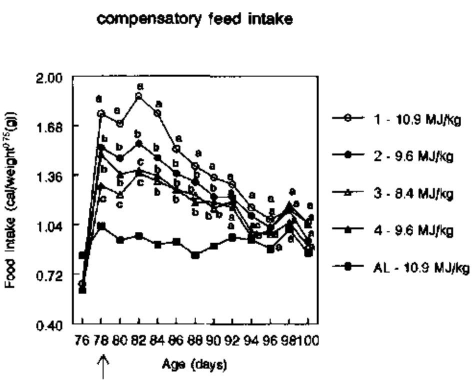

Figure 5. Compensatory feed intake (cal/$g^{0.75}$) in the feed intake motivation test (means of 12 birds per treatment group). $^{a-c}$ Different letters indicate significant differences among treatments (P<0.05). The arrow indicates the start of the test.

Compensatory Feed Intake

The observations of bird behaviour were supported by the results of the feed intake motivation test, showing that the compensatory feed intake over a 3-week period was lowest for birds of treatment 3. Previously it has been shown that the long-term compensatory feed intake is an indicator of hunger in broiler breeders (De Jong et al., 2003). The compensatory feed intakes of birds of treatments 4 and 2 were also lower as compared with treatment 1, indicating that these birds were also less hungry as compared with birds of treatment 1, however, no differences in object pecking and activity were found between treatments 1 and treatment 2 and 4.

Physiological Parameters

Previous research has indicated that plasma corticosteronee concentrations increase when birds are fed at a restriction level of more than 50% of ad libitum during rearing (De Jong et al., 2003). Here, no differences were found in plasma corticosteronee levels among treatments during rearing, and these levels were within the same range as levels of birds fed at the standard restriction level of 35% (De Jong et al., 2002; De Jong et al., 2003). Thus, measurements of plasma corticosteronee concentrations did not support the above conclusion that the low-density diets used in this study reduced hunger at the beginning of the rearing period. In the laying period no differences were found in plasma corticosteronee concentrations.

Previously we reported that the glucose/NEFA ratio increases with increased restriction, indicating that this may be a good parameter of hunger (De Jong et al., 2003). This was caused by lower NEFA concentrations in birds fed at higher restriction levels (i.e., in birds that were hungrier). However, in this experiment, we compared birds fed diets with levels of fiber, which may have affected the passage rate through the gastrointestinal tract as well as levels of circulating glucose and NEFA. Differences in glucose/NEFA ratios and glucose and NEFA levels in plasma were, therefore, more difficult to interpret in terms of hunger. A 24-h profile of glucose and NEFA may give better information about passage rates and metabolic rates.

No differences were found in H/L during rearing, which suggests that there were no differences in level of stress among treatments (Gross and Siegel, 1983). Birds of treatment group 3 had a higher H/L at 40 weeks of age, indicating that these birds might have suffered from chronic stress as compared with those of the other treatments (Gross and Siegel, 1983; Maxwell et al., 1992; Hocking, 1993; Savory and Maros, 1993; Hocking et al., 1996). Birds of treatment 3 needed a long time to consume their feed and thus might have felt satiated much later then those on the other treatments. The long time needed to satisfy birds of treatment 3 may thus explain the higher H/L in these birds. However, it should be recognized that the H/L is not an unequivocal indicator of stress in broiler breeders (De Jong et al., 2002), which indicates that we should be careful to draw conclusions based on this parameter only.

Conclusions

In contrast to previous experiments (Savory et al., 1996; Savory and Lariviere, 2000), but in line with a report of Zuidhof et al. (1995), results of the present experiment indicated that a low-density diet may have a small positive effect on broiler breeder welfare. Behavioural data and the results of the feed intake motivation test indicated that birds of treatment 3 might experience less frustration and hunger as compared with birds of the other treatments. However, these observations were not supported by physiological indicators of hunger and stress. Moreover, positive effects were only found during the first half of the rearing period. Positive effects were small as the birds still performed stereotypic object pecking during a large part of the observation time, indicating that birds still suffer from hunger and frustration of the feeding motivation (Savory and Maros, 1993; Hocking et al., 1996; Savory and Kostal, 1996). Our results indicated that with such severe restriction levels as applied in broiler breeders, it is very difficult to alleviate hunger and frustration as the total energy supplied to the birds should not change. It should be questioned whether bird welfare is indeed improved when differences in hunger and frustration are small and only present during the first half of the rearing period. In the laying period, treatment 3 might even have a negative effect on bird welfare due to the very long feed intake. Treatments 2 and 4 did not seem to have any positive effects on hunger and frustration of the feeding motivation.

Results showed that the energy content of a diet should be substantially reduced to improve broiler breeder welfare during rearing. It should be noted however, that a larger reduction of energy content as applied here may have adverse side effects (e.g., on feed costs, litter quality, and excreta production) and may therefore not be practically applicable (Savory et al., 1996), although we found that only treatment 4 had a negative effect on litter quality (H. Enting, 2003, Schothorst Feed Research, Lelystad, The Netherlands, personal communication). The question remains why we found positive effects of low-density diets here, whereas others (Savory et al., 1996; Savory and Lariviere, 2000) did not find any positive effects of such diets. The exact composition of the diet may explain the differences, as nutrients may not only promote a filled gastrointestinal tract but also satiety. Further research should be carried out to determine if the nutrients we used in the diets might indeed promote feelings of satiety.

We conclude that in the short term broiler breeder welfare during rearing may benefit from diet dilution as described here, but that for a more substantial improvement of broiler breeder welfare during rearing we should look for other solutions. In contrast to the rearing period, the diet with the lowest energy content should not be used during the laying period.

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Chapter 4

The effect of low-density diets on broiler breeder development and nutrient digestibility during the rearing period

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Abstract

Effects of low-density diets on nutrient digestibility and broiler breeder development were studied until the start of the laying period, using Cobb 500 birds. The experiment included 5 treatments. The treatments involved a control group with a normal density diet (ND, 10.88 MJ AME/kg). Treatments 2 and 3 had a 12 and 23% lower nutrient density than ND (LD12 and LD23). This was obtained by inclusion of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal. Treatment 4 also had a 12 % lower nutrient density than ND. This diet was obtained by inclusion of oats and sugar beet pulp (LD12^OP). In the treatments with low-density diets, total daily intake of first limiting nutrients was kept constant by lowering the contents of these nutrients to the same ratio as the energy level. Animal performance, development of the intestinal tract and reproductive tract were determined in addition to digestibility and feed passage rate.

Feeding LD12^OP diets resulted in a lower digestibility of the diet than was calculated and was related to lower live weights. Birds given LD23 and LD12^OP showed a significantly faster ovarium and oviduct development between week 24 and 26. At 22 weeks of age, LD23 and LD12^OP diets gave significantly higher empty jejunum and ileum weights. Low-density diets did not affect intestinal tract contents and decreased mean retention time of the contents. It was concluded that low-density diets can affect live weight and development of digestive and reproductive tracts. These changes were related to a lower digestibility and utilization of digested nutrients with low-density diets.

Introduction

In order to prevent health and reproduction disorders, broiler breeders with a high growth potential are fed restrictedly during the rearing and laying period. In this way, health and reproduction disorders are reduced (Katanbaf et al., 1989a; Hocking et al., 1994). The restriction in nutrient intake is particularly strong during the rearing period. In current feeding programmes for broiler breeders, the daily energy intake can be restricted to 1.3 times the maintenance requirement between 12 and 15 weeks of age. This level of restriction is equivalent to about one-third of the ad libitum feed intake capacity (Savory et al., 1996; De Jong et al., 2002). Severe feed restriction during the rearing period can result in increased corticosterone levels and increased heterophil to lymphocyte (HL) ratios in blood plasma of broiler breeders (Savory et al., 1996). Furthermore, it can increase stereotypic object pecking, hyperactivity (De Jong et al., 2003) and feed intake motivation (Ehlhardt et al., 1997). These changes indicate the occurrence of chronic stress and of hunger feeling (Gross and Siegel, 1983, 1986; Hocking et al., 1993; Savory et al., 1996; De Jong et al., 2003).

Feed restriction can be quantitative or qualitative. The latter one has drawn specific interest because it may alleviate or reduce welfare problems in broiler breeders at higher amounts. By dilution of diets, animals are restricted in nutrient intake at higher feed intake levels. In this way, excessive fatness is avoided and reproductive performance can be maintained. Studies with pigs (Brouns et al., 1994; Ramonet et al., 2000) showed that dilution of diets by inert materials or low energy feedstuffs might reduce chronic stress and hunger feeling. De Leeuw (2004) found no effects of low-density diets at higher feed intake levels on sow performance. However, very few systematic studies in broiler breeders in this field have been done and results were contradictory.

Zuidhof et al. (1995) diluted broiler breeders diets with 15 or 30 % oat hulls and found a reduction in stereotypic behaviour and H/L ratios compared with birds on similar nutrient intake levels from normal density diets. Savory et al. (1996) and Savory and Lariviere (2000) diluted diets with different fibre rich feedstuffs or softwood sawdust. They concluded that these forms of qualitative feed restriction did not affect broiler breeder welfare.

In a recent experiment (Smulders and Enting, unpublished), nutrient density in broiler breeder diets was reduced with 12 and 23 %. The intake of first limiting nutrients was kept constant by an increase in feed allowance. Lowering the dietary nutrient density, a significant reduction in H/L-ratios was observed at six weeks of age. Also a significant reduction in mortality of their offspring was found. This suggests that chronic stress levels can be decreased on low-density diets. Therefore, a study was carried out in which effects of low-density diets with different fibre sources on stress, behaviour, performance and offspring vitality were studied. Results of breeder performance during the rearing period and nutrient digestibility are presented in this paper.

Material and methods

Animals and housing

The protocol for the experiments was in agreement with standards for animal experiments and was approved by the Ethical Committee of Schothorst Feed Research. A total of 2,700 one-day-old Cobb 500 female broiler breeders (Cobb Europe, Putten, The Netherlands) were used. Animals were placed in 30 floor pens of 4.5 x 3 m each with 90 chickens per pen. These pens were located in two identical light-tight compartments (15 pens per compartment). Wood shavings (135 l per pen) were used as floor material. Each treatment was applied in 6 pens from 4 to 24 weeks of age, with pen as block. One treatment (LD12 with a12 % diluted diet) included a double number of replicates, since this treatment was followed by two different treatments during the laying period (Enting et al., 2005).

In week 20, 120 female broiler breeders, 5 taken per pen, were selected at random and placed in digestibility cages in another light-tight compartment. Per digestibility cage, two broiler breeders were housed and three cages formed one replicate. Each treatment involved five replicates in the digestibility study.

Light and temperature schedules were according to advices of the breeder. Lights went on at 07.45 h and were turned of as the recommended day length was reached. A light intensity of 5 lux was applied at animal level. Birds were vaccinated according to the standard vaccination programme of De Kuikenaer Opfok (Delden, The Netherlands) and beaks were trimmed at day 4.

Feed and water supply

In the floor pens, feed was given once a day at 08.00 h. Per pen 5 feeders were available. The amount of feed given to the birds was in accordance with advices of the breeder (Table 1). When live weight of birds deviated more than 5 % from the recommended weights, the feeding level was adjusted.

Water was available via one bell-type drinker per pen. Water was given from half an hour before feed supply until half an hour after feed was consumed in the pen with the longest feed consumption time. In the digestibility study, water intake was restricted to 2.5 times the feed intake.

Table 1. Target live weight, feed allowance and energy intake above maintenance requirement of Cobb 500 female broiler breeders during the rearing period

Week	Target live weight[1]	Feed allowance/day[1]	Maintenance requirement, kJ/day[2]	Energy intake, kJ/day[3]	Energy intake/ maintenance requirement
3	360	40	209	469	2.24
6	750	53	363	621	1.71
9	1,035	58	462	679	1.47
12	1,280	61	542	715	1.32
15	1,580	69	634	808	1.27
18	1,960	88	745	1,031	1.38
22	2,550	125	908	1,464	1.61

[1] Cobb 500 breeder management guide 1997.
[2] 450 kJ x live weight$^{0.75}$ (kg).
[3] Based on an AME content of 11.72 MJ/kg (WPSA basis), which equals 10.88 MJ/kg in the Dutch feed evaluation system for growing chickens (CVB, 2003).

Dietary treatments

The experiment included four treatments, which are presented in Table 2. From week 0-3, all birds were given the same standard phase 1 diet. After that the treatment diets were given. In treatment 1, standard phase 1 and phase 2 broiler breeder pullet diets were given in week 3-6 and in week 6-24 respectively (ND - normal density). In treatment 2 and 3, the nutrient density of the diets was lowered by 12 (LD12) and 23 % (LD23) respectively. This was done by inclusion of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal in these diets. The lower densities were chosen on the basis of preliminary studies done before. Treatment 4 included diets in which the nutrient density was decreased by 12 % using oats and sugar beet pulp ($LD12^{OP}$) instead of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal.

Table 2. *Overview of treatments during the rearing period*

Treatment[1]	Weeks 0-3	Weeks 4-24
1		ND
2	ND	LD12
3		LD23
4		$LD12^{OP}$

[1] ND - normal nutrient density, LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, $LD12^{OP}$ - 12 % lower nutrient density with other feedstuffs than in LD12

Measurements

Feed intake and mortality were recorded on a daily basis. Live weight of birds was determined every 3 weeks. From week 18 onwards, two birds were sacrificed at random per week to determine the time at which the ovarium and oviduct started to develop. In week 24 and 26, 2 birds of every replicate were sacrificed by cervical dislocation and the weight of the bird, oviduct and ovarium were recorded, as was oviduct length.

After an adaptation period of two weeks, excreta were collected semi-quantitatively in the digestibility study during four consecutive days. Excreta were collected twice a day and samples were pooled per replicate. During the period of excreta sampling, feed samples were taken every day. These samples were pooled for four days. In feeds and excreta, dry matter, crude protein, crude ash, crude fat, crude fibre and gross energy were determined according to ISO 6496 (ISO 1999b), ISO/DIS 16634 (ISO, 2004), ISO 5984 (ISO, 1978a), ISO 6492 (ISO, 1999a), NEN 5417 (NNI, 1988) and ISO 9831 (ISO, 1998). Acid insoluble ash was determined as a marker for digestibility according to ISO 5985 (ISO, 1978b). Similar to the performance study, feed was given once a day at 08.00 h in the digestibility study.

At the end of the excreta collection period, all six birds per replicate were sacrificed between one and seven hours after feeding by injection of 0,5 ml T61® (200 mg embutramide, 50 mg mebezoniumiodide and 5 mg tetracainehydrochloride per ml, Intervet, Boxmeer, The Netherlands) in the wing vein. The alimentary tract was removed after euthanasia. Crop, proventriculus and gizzard, duodenum, jejunum, ileum, caeca and colon were separated and weighed. The intestinal contents were collected by gently stripping and weighed. Intestinal contents of two birds were pooled, so that three samples per replicate were obtained. Mean retention time (MRT) of the feed in the different sections of the alimentary tract was calculated according to Weurding et al. (2001).

Table 3. Composition and calculated contents of the experimental diets (g/kg)

Period, week	Weeks 4-6			Weeks 7-24		
Diet[1]	ND	LD23	LD12^{OP}	ND	LD23	LD12^{OP}
$AME_{broilers}$[2], MJ/kg	10.88	8.37	9.62	10.88	8.37	9.62
Corn	250.0	250.0	250.0	250.0	250.0	250.0
Wheat	347.8	63.7	117.9	318.4	97.1	173.6
Oats			150.0			150.0
Soya bean meal	137.4	18.3	165.9	101.2		143.9
Sunflower seed meal	43.4	125.0		14.8	125.0	
Rapeseed meal	30.0	30.0	30.0	30.0	30.0	30.0
Animal fat	6.6			26.3		
Soya bean oil	15.2	5.0	11.7	6.5		5.1
Corn gluten feed	100.0	100.0		100.0	100.0	
Palm kernel meal		100.0			100.0	
Sugar beet pulp			150.0			150.0
Wheat bran		125.0	36.2	100.0	125.0	54.1
Wheat gluten feed		100.0	23.7		100.0	
Lucerne		28.8			29.3	
Sugar cane molasses	20.0	20.0	20.0	20.0	20.0	20.0
Chalk/limestone	12.5	9.7	8.3	9.3	6.1	4.9
Monocalcium phosphate	6.7	0.9	9.4	0.7		5.4
Premix, vitamins and minerals[3]	5.0	5.0	5.0	5.0	5.0	5.0
Premix, lysine+methionine	10.8		5.3	3.6		0.4
Premix, lysine		8.5		2.4	5.3	
Premix, methionine	2.7		8.9			0.1
Premix, phytase[4]	4.0	4.0	0.3	4.0	1.1	
Premix, acid	5.0	5.0	5.0	5.0	5.0	5.0
Salt	2.8	1.1	2.5	2.8	1.0	2.6
Total	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0
Calculated contents						
Dry matter	874	882	879	873	881	876
Ash	56	59	59	48	53	51
Crude protein	174	165	167	157	158	157
Digestible lysine	8.4	6.4	7.4	6.7	5.2	5.9
Digestible methionine+cystine	7.1	5.5	6.5	5.7	5.3	5.0
Crude fat	44	41	38	57	36	31
Linoleic acid	18	14	16	16	12	13
Crude fibre	40	90	65	40	90	65
Calcium	8.9	7.7	8.3	6.5	5.8	6.2
Phosphorus	5.9	6.6	5.9	5.0	6.4	5.0
Retainable phosphorus	3.7	2.9	3.3	2.6	2.2	2.4
Sodium	1.6	1.2	1.4	1.6	1.2	1.4
In vitro viscosity, mPa.s[5]	3.1	2.8	5.8	2.9	3.5	5.9

1) ND - normal nutrient density, LD23 - 23 % lower nutrient density, LD12^{OP} - 12 % lower nutrient density with other feedstuffs than in LD12 (LD12 was obtained by mixing equal amount of ND and LD23).

2) CVB, 2003.

3) This premix supplied per kg of feed 8.750 IU vitamin A, 1500 IU vitamin D_3, 12.5 IU vitamin E, 1 mg vitamin K_3, 3 mg vitamin B_2, 6 mg pantothenic acid, 15 mg niacin, 1 mg vitamin B_6, 0,75 mg folic acid, 0,015 mg vitamin B_{12}, 50 mg biotin and 200 mg choline.

4) This premix supplied 500 FTU phytase per kg of feed (Natuphos, DSM, Delft, The Netherlands).

5) Determined according to Bedford and Classen, 1993.

Diet composition

The compositions and calculated contents of the ND, LD23 and $LD12^{OP}$ diets are presented in Table 3. The composition of the LD12 diets in terms of nutrient density was intermediate to that of ND and LD23. The control diet ND contained corn, wheat, soya bean meal and corn gluten feed as major ingredients and an AME content 10.88 MJ/kg. It contained 174 g/kg crude protein in the first phase (4-6 weeks of age) and 157 g/kg in the second phase (7-24 weeks of age). In the low-density diets, digestible lysine, calcium, retainable phosphorus and linoleic acid were lowered to the same extend as AME. The amount of feed offered in LD12, LD23 and $LD12^{OP}$ was increased by the same percentage as the AME content of the feed was decreased compared with ND. In this way, a similar daily intake of first limiting nutrients was obtained for the different treatments. Feeds were given as mash and were milled with a 3 mm screen to have similar particle sizes in feeds. In the digestibility study, 3 % insoluble ash and 0.15 % Cr_2O_3 were added as markers on top of the diets presented in Table 3.

Statistical analysis

Data were analysed by analysis of variance with block and treatment as factors (general linear models procedure of GenStat 7.1, GenStat Committee, 2003). Output data were expressed as means with standard error of means. Treatments were compared by least significant differences (Snedecor and Cochran, 1967). Parameters were tested for normal distributions before analyses. Differences between treatments were considered significant at $P \leq 0.05$.

Results

Bird performance

Results of live weight and feed intake of broiler breeder hens are presented in Table 4. At the end of the rearing period, the target weight of 2,550 grams (Table 1) was nearly reached in birds given ND, LD12 and LD23. In weeks 6, 12 and 18, live weight in hens given LD23 was significantly higher than in hens fed ND, giving significant linear relationships between live weight and AME content. $LD12^{OP}$ gave a significantly lower live weight at the end of the rearing period compared with ND. The difference in growth rate between birds given ND and $LD12^{OP}$ became significant after 18 weeks of age. Mortality was low during the entire rearing period (2.2 %) and almost absent during the first six weeks (0.1 %).

Anatomical composition

The empty weight of the proventriculus and gizzard was significantly higher in birds given LD12 compared with birds on ND (Table 5). Birds fed LD23 had significantly heavier jejunum and ileum than ND given birds. Compared with ND, also LD12[OP] gave significantly higher jejunum and ileum weights. The colon weight in this treatment was significantly higher in comparison with the other treatments.

Table 4. Effect of low-density diets on live weight and feed intake in different treatments during the rearing period

Treatment[1)]	ND	LD12	LD23	LD12[OP]	SEM
Live weight, g					
Week 6	922^{a}	923^{a}	955^{b}	949^{b}	4
Week 12	1,476^{a}	1,478^{a}	1,503^{b}	1,482^{a}	3
Week 18	1,966^{b}	1,982^{bc}	1,995^{c}	1,893^{a}	7
Week 22	2,519^{b}	2,517^{b}	2,547^{b}	2,401^{a}	10
Feed intake, g					
Week 0-6	2,022	2,186	2,364	2,194	
Week 0-12	4,129	4,481	5,020	4,486	
Week 0-18	6,585	7,246	8,147	7,252	
Week 0-22	9,113	10,109	11,412	10,185	

[1)] ND - normal nutrient density (10.88 MJ/kg), LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, LD12[OP] - 12 % lower nutrient density with other feedstuffs than in LD12.

The development of reproductive organs until week 24 and 26 is given in Table 6. At week 24, the oviduct weight was significantly lower in hens given LD12[OP] compared with hens on ND and LD12. The length of the oviduct in hens given LD12[OP] was significantly shorter in comparison with all other treatments in this week. At 26 weeks of age, no significant differences in ovarium weight and oviduct length between treatments were found. The oviduct weight in LD23 hens was significantly higher compared with hens given ND at this age. The increase in ovarium weight between week 24 and 26 was significantly higher when LD23 and LD12[OP] were given instead of ND. Increases in oviduct weight and length were significantly higher on LD12[OP] compared with ND.

Table 5. Effect of low-density diets on weight of empty parts (g) of the digestive tract in week 22

Treatment[1)]	ND	LD12	LD23	LD12[OP]	SEM
Crop	86.1	99.9	90.3	89.0	3.7
Proventriculus+gizzard	25.8^{a}	31.9^{b}	31.2^{ab}	30.6^{ab}	1.5
Duodenum	3.4	3.2	3.3	2.5	0.2
Jejunum	11.1^{a}	13.5^{a}	19.5^{b}	20.2^{b}	1.4
Ileum	14.5^{a}	17.6^{a}	23.4^{b}	23.4^{b}	1.3
Caeca	7.6	9.1	8.4	5.5	0.7
Colon	4.0^{a}	3.9^{a}	4.9^{a}	6.4^{b}	0.3

[1)] ND - normal nutrient density (10.88 MJ/kg), LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, LD12[OP] - 12 % lower nutrient density with other feedstuffs than in LD12.

Digestibility and passage rate

Digestibility coefficients of all nutrients and AME_N contents were significantly lower when nutrient density of the diets decreased (Table 7). $LD12^{OP}$ gave significantly lower digestibility coefficients for organic matter, crude fat and NFE compared with LD12. Also the determined AME_N content of $LD12^{OP}$ was significantly lower than of LD12. The determined AME_N levels of ND, LD12 and LD23 were higher than the calculated levels, with the largest difference between the calculated and determined AME_N for LD12.

Table 6. Effect of low-density diets on ovarium weight and oviduct weight and length in different treatments at 24 and 26 weeks of age

Treatment[1)]	ND	LD12	LD23	$LD12^{OP}$	SEM
Week 24					
Weight ovarium, g	24.6	23.4	15.9	7.5	2.5
Weight oviduct, g	37.6^{b}	40.5^{b}	33.9^{ab}	18.6^{a}	2.7
Length oviduct, cm	48.5^{b}	49.0^{b}	48.0^{b}	32.8^{a}	1.9
Week 26					
Weight ovarium, g	54.6	60.9	69.2	60.3	2.2
Weight oviduct, g	64.7^{a}	65.1^{ab}	73.9^{b}	68.6^{ab}	1.3
Length oviduct, cm	58.6	61.2	62.1	62.2	1.2
Week 24-26					
Δ weight ovarium, g	30.0^{a}	37.6^{ab}	53.3^{b}	52.8^{b}	3.2
Δ weight oviduct, g	27.1^{a}	24.7^{a}	40.1^{ab}	50.0^{b}	3.0
Δ length oviduct, cm	10.1^{a}	12.2^{a}	14.1^{a}	29.4^{b}	1.8

1) ND - normal nutrient density (10.88 MJ/kg), LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, $LD12^{OP}$ - 12 % lower nutrient density with other feedstuffs than in LD12

Table 7. Effect of low-density diets on digestibility coefficients of organic matter, crude protein, crude fat and NFE and AME content of the experimental diets

Treatment[1)]	ND	LD12	LD23	$LD12^{OP}$	SEM
AME, calculated, MJ/kg	10.88	9.62	8.37	9.62	
Digestibility coefficient					
Organic matter	76.4^{d}	72.0^{c}	62.2^{a}	68.4^{b}	1.3
Crude protein	82.5^{b}	81.0^{ab}	79.9^{a}	81.9^{b}	0.3
Crude fat	79.6^{d}	76.1^{c}	68.5^{b}	64.5^{a}	1.5
NFE	80.4^{d}	77.6^{c}	66.4^{a}	73.9^{b}	1.2
AME_N, MJ/kg[2)]	11.37^{d}	10.59^{c}	9.12^{a}	9.86^{b}	0.24

1) ND - normal nutrient density (10.88 MJ/kg), LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, $LD12^{OP}$ - 12 % lower nutrient density with other feedstuffs than in LD12.
2) AME level at N-retention zero.

Table 8 presents the contents of different parts of the alimentary tract for the different treatments. The highest amounts of chyme were found in proventriculus and gizzard. In treatment LD12, LD23 and $LD12^{OP}$, a significantly higher ileum content was found compared with hens given ND.

Table 8. Effect of low-density diets on contents (g) of different parts of the alimentary tract in week 22

Treatment[1)]	ND	LD12	LD23	$LD12^{OP}$	SEM
Crop	10.2	11.0	11.3	10.7	0.2
Proventriculus+gizzard	41.7	46.4	43.2	42.1	1.2
Duodenum	16.2	16.8	14.4	15.2	0.4
Jejunum	17.8	19.1	18.2	17.2	0.5
Ileum	11.1^{a}	14.6^{b}	13.2^{b}	14.7^{b}	0.5
Caeca	8.8	12.3	10.0	9.8	0.8
Colon	4.0	4.6	4.3	4.9	0.2

[1)] ND - normal nutrient density (10.88 MJ/kg), LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, $LD12^{OP}$ - 12 % lower nutrient density with other feedstuffs than in LD12.

The mean retention times (MRT) of the feed in different parts of the alimentary tract are given in Table 9. Low-density diets gave shorter MRT's in almost all sections of the alimentary tract. Significant differences of MRT between treatments were observed in jejunum and colon. Compared with LD12, $LD12^{OP}$ gave a significantly longer MRT in the caeca.

Table 9. Effect of low-density diets on mean retention times (minutes) of different parts of the alimentary tract in week 22

Treatment[1)]	ND	LD12	LD23	$LD12^{OP}$	SEM
Crop	148	117	108	135	49
Proventriculus+gizzard	218	223	189	155	95
Jejunum	542^{b}	395^{a}	339^{a}	388^{a}	132
Ileum	408	360	283	406	178
Caeca	180^{a}	218^{a}	183^{a}	390^{b}	82
Colon	222^{b}	134^{a}	94^{a}	161^{a}	76

[1)] ND - normal nutrient density (10.88 MJ/kg), LD12 - 12 % lower nutrient density, LD23 - 23 % lower nutrient density, $LD12^{OP}$ - 12 % lower nutrient density with other feedstuffs than in LD12

Discussion

The supply of low-density diets based on similar calculated AME intakes resulted in similar live weights at the end of the rearing period, except for $LD12^{OP}$. The latter was attributed to the lower than expected AME intake of $LD12^{OP}$. The determined AME intake on this diet was 4 % lower in comparison with ND. Although hens given LD12 had a 3.1 % higher total AME intake compared with hens given ND, no differences in live weight were observed between these treatments. This is probably due to a similar total intake of first limiting digestible amino acids in birds given LD12 and ND.
The digestibility experiment showed a higher AME content of LD12 than expected, which might be related the relatively longer MRT in different parts of the digestive tract in hens given LD12. Rogel (1997) observed an increased starch digestibility when oat hulls were included in the feed. Svihus and Hetland (2001) found a similar

positive effect on starch digestibility when diets were diluted with cellulose. Combined with the results of the present study, it can be concluded that the inclusion of some fibre rich feedstuffs may result in higher digestibility coefficients and AME content than expected. It should be noted that this effect is dependent on dietary fibre type, since the inclusion of oats and sugar beet pulp had a negative effect on nutrient digestibility. With a high content of fibre as in LD23 however, no higher digestibility coefficients and AME were observed. They observed differences in determined nutrient intake between treatments emphasizes the importance of digestibility studies when effects of low-density diets on performance are studied. These differences may have carry over effects on laying performance (Enting et al., submitted).

Besides differences in live weight gain between treatments, also significant differences were found in anatomical composition at the end of the rearing period of 22 weeks. Significantly higher gizzard, jejunum and ileum weights were found when low-density diets had been given. This indicates a better intestinal development, which is probably related to more work due to transport of feed through the intestinal tract. Similar effects were found on gizzard weight by Svihus et al. (1997), who compared whole with ground barley in broiler chicken diets.

In hens given LD23 and particularly in $LD12^{OP}$ birds, reproductive development was delayed in week 24. In week 26 however, differences in development had disappeared. This was the result of differences in growth rate of the reproductive tract between week 24 and 26. The delay in onset of growth of the reproductive tract resembles the delay in onset that has been obtained with a more restricted feed intake or day length during rearing (Kwakkel et al., 1995; Hocking, 1996; Bruggeman et al., 1999; Hocking and Robertson, 2000). Katanbaf et al. (1989b) observed a higher oviduct weight at onset of laying when feed intake of broiler breeders had been restricted more severely. Fattori et al. (1990; 1993) showed that even small reductions in nutrient intake can delay the development of the reproductive tract, which might explain the delayed onset of growth of the reproductive tract in hens given $LD12^{OP}$ compared with hens on ND. However, this can not explain the delayed onset in birds given LD23, since AME intake was equal to that in birds fed ND. On the basis of the results of the digestibility study, the digestible crude protein intake in LD23 hens was higher than in ND birds, but the total digestible lysine and methionine+cystine intake were similar between these treatments. Therefore, it might have been possible that a larger proportion of protein was used for energy in birds given LD23, resulting in a lower net energy intake compared with hens on ND. A direct effect of the increased ratio between digestible protein and AME intake in LD23 birds compared with ND birds might be another explanation for the delay in reproductive tract development. However, there is no foundation for this.

Kwakkel et al. (1991; 1995) found that differences in the development of different tissues in rearing birds due to differences in nutrient intake without clear differences in live weight can affect laying performance. This implies that feeding of low-density diets during rearing might have an effect on performance during the laying period. Data of the digestibility study showed that relative differences in the contents of the alimentary tract between treatments were smaller than differences in feed intake. This was not related to the fibre type in diets, because no significant differences were found between LD12 and LD12^{OP}. The amount of chyme in crop, proventriculus and gizzard was fairly constant between treatments. Birds compensated the higher feed intake on low-density diets by a shorter MRT of the feed in the different compartments of the alimentary tract. An exception to this was the MRT in the caeca in hens given LD12^{OP}. This effect can be attributed to the higher viscosity of these diets (Smits, 1997). It may also have resulted from more fermentation of this fibrous diet.

The absence in changes in alimentary tract contents and the reduction of the MRT with low-density diets, might indicate that these diets lack impact on satiety and hunger feeling. However, De Jong et al. (2005) found a significant reduction in stereotypic pecking behaviour and a significant increase in the time spent sitting in hens given LD23 during the first half of the rearing period. Furthermore, they found that birds on LD23 consumed less energy in the feed intake motivation test compared with birds given ND and LD12^{OP} birds consumed less than birds fed LD12. These findings indicate that LD23 and LD12^{OP} diets can increase satiety and might give a reduction in hunger feeling. However, this higher degree of satiety is probably only detected by birds in an ad libitum feed intake situation like in the feed intake motivation test used by De Jong et al. (2005) and at relatively high feed intake levels compared with the ad libitum feed intake capacity. De Jong et al. (2005) found no effects of low-density diets on behaviour when feed intake levels during rearing were below 1.5 times the maintenance requirement for energy.

Based on the results obtained in this study, it can be concluded that low-density diets can affect live weight and development of the digestive and reproductive tract. The changes in these parameters can be related to a lower in digestibility and lower utilization of digested nutrients on low-density diets.

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Chapter 5

The effect of low-density diets on broiler breeder performance during the laying period and on embryonic development of their offspring

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Abstract

The impact of low-density diets on bird performance, egg composition and embryonic development was studied with Cobb broiler breeders of 25 to 60 weeks of age. The experiment included 5 treatments. The treatments included a control group with a normal density diet (ND, 11.72 MJ AME/kg). Treatments 2 and 3 had a 11 and 21% lower nutrient density (LD11 and LD21). This was obtained by inclusion of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal. Treatment 4 also had a 11 % less dense diet, which was obtained by inclusion of oats and sugar beet pulp ($LD11^{OP}$). In these treatments similar diets were given during the rearing and the laying period. An additional treatment 5 combined LD12 in the rearing period and ND diets during the laying period (LD12-ND). In treatments with low-density diets, the ratio of first limiting nutrients to energy was kept constant. Development and egg weight of all birds were determined. Egg composition and embryonic development were measured in eggs of ND and LD21 birds at 29 and 41 weeks of age.

During the laying period, birds had similar live weights in the different treatments, except for birds given $LD11^{OP}$, which had lower live weights. LD11 gave a significantly higher rate of lay compared with ND. Egg weights were significantly higher when low-density diets were given, particularly when $LD11^{OP}$ was fed. LD21 gave a better development of the area vitellina externa and heart and embryo weight at 29 weeks of age. It was concluded that this was related to the higher egg weight and egg white proportion when LD21 was given. This suggests that the amount of egg white in eggs of hens given ND was limiting for embryonic development, particularly in eggs of young broiler breeders.

Introduction

Live weight gain is an important feature in selection programmes for broiler chicken parent stock. This parameter has however a negative relation with reproductive performance (Hocking, 1994). High live weight gain and fat deposition during the rearing period can lead to reproduction disorders during the laying period. In order to prevent this, feed intake is restricted in broiler chicken parent stock. The current high levels of feed restriction can induce hunger feeling and this may impair animal welfare (Hocking et al., 1993; Savory et al., 1996; De Jong et al., 2003). The daily energy intake during rearing can be restricted to a maximum of 1.3 to 1.4 times maintenance (Enting et al., submitted). This equals about one-third of the ad libitum feed intake (Savory et al., 1996; De Jong et al., 2003). During the laying period, daily energy intake is restricted to 1.6 times maintenance as an average, which equals about 70 to 100 % of the ad libitum feed intake (De Jong et al., 2003).

In order to alleviate effects of feed restriction on hunger feeling of broiler breeders, low-density diets have been investigated during the rearing period. Sofar, contradictory effects of these diets on animal welfare have been reported (Zuidhof et al., 1995; Savory et al., 1996; Savory and Lariviere, 2000; De Jong et al., 2005). Effects of low-density diets on animal welfare and performance during the laying period have been studied on a limited scale (Zuidhof et al., 1995; De Jong et al., 2005).

In addition to possible effects of low-density diets on hunger feeling, Smulders and Enting (unpublished) observed increased weights of eggs and day-old chickens when broiler breeders were given low-density diets. These broiler chickens had a higher initial growth rate and a significantly lower mortality rate compared to broiler chickens from parents given normal density diets. In vitro embryo production studies in dairy cattle and sheep have shown that in vitro growth conditions can affect performance, vitality ad mortality of offspring (Walker et al., 1992; 1996; Farin and Farin, 1995; Kruip and Den Daas, 1997). Wilmut and Sales (1981) and Kleemann et al. (1995) found that foetal development and animal health in dairy cattle and sheep can be influenced by growth conditions in the uterus.

When hatching conditions and egg composition are compared with in vitro and uterine growth conditions in for instance dairy cattle and sheep, it is hypothesized that egg size and egg composition can affect embryonic development and subsequent broiler chicken performance and mortality. Therefore, an experiment with various low-density broiler breeder diets was performed to investigate egg weight, egg composition and embryonic development in addition to broiler breeder performance.

Material and methods

Animals and housing

The protocol for the experiment was in agreement with standards for animal experiments and was approved by the Ethical Committee of Schothorst Feed Research. The experiment involved a total of 2,100 Cobb 500 female and 210 Cobb 500 male broiler breeders. The female birds were raised at Schothorst Feed Research. Male birds of 25 weeks old were obtained from De Kuikenaer Opfok (Delden, The Netherlands). During rearing, light, temperature, live weight and feed allocation schedules of the breeder (Cobb-Europe, Putten, The Netherlands) were used for both female and male birds.

During the laying period, birds were housed in 30 floor pens of 4.5 x 3 m with 70 female and 7 male birds per pen. These pens were located in two identical light-tight compartments (15 pens per compartment). Each pen was equipped with 4 laying nests of 95 x 32 x 34 cm. Each treatment included 6 pens with pen as block.

Wood shavings were used as floor material (135 l per pen). Light and temperature schedules were according to advices of the breeding company (Cobb Europe, Putten, The Netherlands). Lights were switched on at 07.45 h and were turned of as the recommended day length was obtained. Vaccination of birds during the laying period was according to the standard vaccination programme of De Kuikenaer (Delden, The Netherlands).

Feed and water supply

Feed was given by one feeding line per pen, fitted with five feeders. Feeds were given once a day at 08.00 h at levels as recommended by the breeder (see Table 1).

Table 1. Target live weight, feed allowance and maintenance requirement of female broiler breeders during the laying period

Week	Target live weight, g[1]	Feed allowance, g/day[1]	Maintenance requirement, kJ/day[2]	Energy intake, kJ/day[3]	Energy intake/ maintenance requirement
25	3,050	145	1,039	1,699	1.64
30	3,410	168	1,129	1,968	1.74
40	3,540	162	1,161	1,898	1.63
50	3,670	152	1,193	1,781	1.49
60	3,800	142	1,225	1,663	1.36

1) Cobb 500 breeder management guide 1997

2) 450 kJ x live weight$^{0.75}$ (kg)

3) Based on an AME content of 11.72 MJ/kg (calculated according to CVB, 2003).

Water was available by one bell-type drinker per pen from half an hour before feed allowance until half an hour after the last pen had consumed the amount of feed given. In treatments with low-density diets, feed allowance was increased to provide the same AME intake in all treatments.

Dietary treatments

Table 2 represents the treatments included in the experiment. In treatment 1, a standard broiler breeder diet was given with a calculated AME content of 11.72 MJ/kg (ND). Treatments 2 and 3 had a 11 and 21 % lower AME density (LD11 and LD21). The density of first limiting nutrients in the diet of these treatments was also decreased by 11 and 21 % respectively. These lower densities were selected on the basis of results of a preliminary study (Smulders and Enting, unpublished). The lower nutrient densities were obtained by the inclusion of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal in the diet. Treatment 4 included a 11 % lower dense diet in which the nutrient density was decreased by inclusion of oats and sugar beet pulp (LD11^{OP}). Since in our preliminary study no increase in egg weight and no decreased offspring mortality were found when low-density diets were given during the laying period only (Smulders and Enting, unpublished), one additional treatment 5 was included (LD12-ND). In this treatment, a low-density diet was given during the rearing period and a normal density diet during the laying period.

Table 2. Overview of treatments; treatments during the rearing period are also presented (Enting et al., submitted)

Treatment[1)]	Weeks 0-3	Weeks 4-24	Weeks 25-60
1		ND	ND
2		LD12	LD11
3	ND	LD23	LD21
4		LD12^{OP}	LD11^{OP}
5		LD12	ND

[1)] ND - normal nutrient density, LD11 - 11 % lower nutrient density, LD21 - 21 % lower nutrient density, LD11^{OP} - 11 % lower nutrient density with other feedstuffs.

Measurements

Feed intake, rate of lay, egg weight and mortality were recorded daily. Live weight of birds was recorded at 25, 30, 40, 50 and 58 weeks of age. The percentage of fertilized and hatched eggs were determined every two weeks from 25 to 58 weeks by hatching each time 150 eggs per replicate at a commercial hatchery (Cobroed, Lievelde, The Netherlands). In addition, at 29 and 41 weeks of age, 40 eggs per replicate of birds given ND and LD21 were hatched at the Animal Science Group, Lelystad, The Netherlands. After 24, 36, 48, 72, 84 and 264 hours of incubation, the development of the embryo's was measured in respectively 50, 50, 30, 30, 30 and 50 eggs per treatment according to Hamilton (1952). The development of the area vitellina externa, the area vasculosa and heart and embryo weights were measured. In eggs in which the embryonic development was measured, the white/yolk ratio was determined as well.

Diet composition

The composition and calculated contents of the diets are given in Table 3. The composition of LD11 diets was intermediate to those of ND and LD21. The ND diets had corn, wheat, soya bean meal and corn gluten feed and wheat bran as major ingredients and contained 11.72 MJ AME/kg. Crude protein content in the ND diets was 153 g/kg and 139 g/kg from week 25 to 30 and 31 to 60 respectively. The nutrient density of the diets was decreased by either palm kernel meal, wheat gluten feed, and sunflower seed meal in LD11 and LD21 or oats and sugar beet pulp in LD11^{OP}. The content of the first limiting nutrients digestible lysine, calcium, retainable phosphorus and linoleic acid content was decreased with the same ratio as the AME content of the diets. Feeds were given as mash and were milled with a 3 mm screen to have the same in particle size in all diets.

Table 3. Composition and calculated contents of the experimental diets

Period, weeks	Week 25-30			Week 31-60		
Diets[1]	ND	LD21	LD11[OP]	ND	LD21	LD11[OP]
AME_{layers}, MJ/kg[2]	11.72	9.20	10.46	11.72	9.20	10.46
Corn	250.0	250.0	250.0	300.0	300.0	300.0
Wheat	211.6	89.8	130.6	179.3	84.6	99.8
Oats			150.0			150.0
Soya bean meal	114.5		130.4	77.8		102.7
Sunflower seed meal	24.2	133.9	26.9	28.8	104.4	45.7
Rapeseed meal	30.0	30.0	30.0	30.0	30.0	30.0
Animal fat	51.1	1.0	18.6	57.5		23.8
Soya bean oil	6.9	6.7	10.1	1.4	4.7	3.6
Corn gluten feed	100.0	22.4		100.0		
Palm kernel meal		125.0			150.0	
Sugar beet pulp			150.0			125.0
Wheat bran	100.0	125.0		100.0	56.5	10.6
Wheat gluten feed		100.0			100.0	
Lucerne		25.3			40.0	
Sugar cane molasses	20.0	20.0	20.0	20.0	20.0	20.0
Lupins					30.6	
Limestone	67.2	49.4	55.3	81.3	59.4	68.5
Monocalcium phosphate	2.3	0.5	6.5	0.6		2.8
Premix, vitamins and minerals[3]	10.0	10.0	10.0	10.0	10.0	10.0
Premix, lysine	2.1	4.4		3.3	3.1	
Premix, methionine			5.6			
Premix, phytase[4]	4.0	1.6		4.0	1.6	1.6
Premix, acid	5.0	5.0	5.0	5.0	5.0	5.0
Salt	1.1		0.9	1.0	0.1	0.9
Total	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0
Calculated contents, g/kg						
Moisture	115	113	113	113	110	113
Ash	109	96	103	120	103	111
Crude protein	153	148	148	139	143	140
Digestible lysine	6.0	4.7	5.4	5.4	4.3	4.8
Digestible methionine+cystine	5.5	5.3	5.6	5.1	5.0	5.0
Crude fat	80	43	52	82	42	52
Linoleic acid	18	14	16	16	13	15
Crude fibre	40	90	65	40	90	65
Calcium	30.0	23.6	26.8	34.5	27.2	31.0
Phosphorus	5.2	6.0	4.7	4.6	5.0	4.0
Retainable phosphorus	2.8	2.2	2.5	2.6	2.2	2.4
Sodium	1.6	1.2	1.4	1.6	1.2	1.4
In vitro viscosity, mPa.s[5]	2.7	3.0	3.9	2.5	2.5	3.0

[1] ND - normal nutrient density, LD21 - 21 % lower nutrient density, LD11[OP] - 11 % lower nutrient density with other feedstuffs; LD11 was obtained by mixing equal amounts of ND and LD21[1][2].

[2] Calculated according to CVB, 2003.

[3] This premix supplied per kg of feed 12,000 IU vitamin A, 2,100 IU vitamin D_3, 27.5 IU vitamin E, 2 mg vitamin K_3, 1 mg vitamin B_1, 6 mg vitamin B_2, 10 mg pantothenic acid, 20 mg niacin, 2 mg vitamin B_6, 0.8 mg folic acid, 0.020 mg vitamin B_{12}, 0.15 mg biotin and 200 mg choline.

[4] This premix supplied 500 FTU phytase per kg of feed (Natuphos, DSM, Delft, The Netherlands).

[5] Determined according to Bedford and Classen, 1993.

Statistical analysis

Data that were obtained from the broiler breeders in the laying period and were analysed by analysis of variance (general linear models procedure of GenStat 7.1, GenStat Committee, 2003). Block and treatment were used as factors in the statistical model for breeder performance date. The statistical model for egg composition and embryonic development parameters included incubation time besides block and treatment. Parameters were tested for normal distributions before analyses. Embryonic development data were analysed on a logarithmic scale, since this increased residual variance homogeneity substantially. Output data were expressed as means with standard error of means. Significant differences between treatments were indicated by a least significant differences procedure (Snedecor and Cochran, 1967). Differences between treatments were considered significant at $P \leq 0.05$.

Results

Bird performance

Live weights of female and male birds are given in Table 4. Low-density diets gave a significant reduction in live weight of females in week 30 when these diets were fed during both the rearing and laying period. No significant differences in live weight were found in week 25 and 58 between hens on ND, LD11 and LD21. The inclusion of oats and sugar beet pulp in the low-density diets ($LD11^{OP}$) gave significantly lower live weights in female birds compared with all other treatments.
Male live weights were significantly lower with LD21 compared with ND in week 30. In week 25 and 30, male bird weight was significantly lower when $LD11^{OP}$ was given in comparison with ND. ND and LD12-ND gave similar live weights for both female and male birds.

Table 4. Effect of low-density diets on live weights of female and male broiler breeders during the laying period (g)

Treatment[1]	ND	LD11	LD21	$LD11^{OP}$	LD12-ND	SEM
Live weight female birds						
Week 25	$3{,}106^{b}$	$3{,}115^{b}$	$3{,}106^{b}$	$2{,}967^{a}$	$3{,}128^{b}$	11
Week 30	$3{,}544^{d}$	$3{,}493^{c}$	$3{,}423^{b}$	$3{,}343^{a}$	$3{,}528^{cd}$	13
Week 58	$4{,}233^{bc}$	$4{,}338^{c}$	$4{,}253^{bc}$	$4{,}058^{a}$	$4{,}185^{b}$	22
Live weight male birds						
Week 25	$3{,}885^{b}$	$3{,}867^{b}$	$3{,}721^{ab}$	$3{,}627^{a}$	$3{,}811^{ab}$	28
Week 30	$3{,}868^{c}$	$3{,}717^{bc}$	$3{,}485^{a}$	$3{,}592^{ab}$	$3{,}767^{bc}$	35
Week 58	$4{,}395^{ab}$	$4{,}232^{a}$	$4{,}478^{ab}$	$4{,}608^{b}$	$4{,}327^{ab}$	52

[1] ND - normal nutrient density, LD11 - 11 % lower nutrient density, LD21 - 21 % lower nutrient density, $LD11^{OP}$ - 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

Laying performance

LD11 gave a significantly higher rate of lay than ND (Table 5). Peak production in birds given LD21 was reached at a significantly higher age compared with birds on ND and LD11. Egg weight increased significantly with LD11 and LD21 compared with ND. LD11^{OP} gave a significantly lower peak production than ND. The rate of lay during the entire laying period did not differ between these two diets. Compared with all other treatments, egg weight of birds given LD11^{OP} was significantly higher. The rate of lay of birds on LD12-ND was intermediate to that of ND and LD11 birds. LD11 and LD12-ND gave similar egg weights. From week 25 to 30, the difference in egg weight was significant between these two treatments (55.9 for LD12-ND vs. 55.4 gram for ND, $P<0.05$).

Table 5. Effect of low-density diets on feed intake and egg production traits during the period from week 25-60

Treatment[1)]	ND	LD11	LD21	LD11^{OP}	LD12-ND	SEM
Feed intake, g/male/day	140.0	157.1	179.2	160.1	140.8	
Feed intake, g/female/day	156.5	176.2	199.9	178.7	157.5	
Rate of lay, %	57.7^{a}	60.2^{b}	58.0^{ab}	57.1^{a}	59.0^{ab}	0.4
Peak rate of lay, %	81.8^{b}	81.5^{ab}	80.3^{ab}	78.1^{a}	79.7^{ab}	0.5
Age peak production, week	30.5^{a}	30.3^{a}	32.3^{b}	31.8^{ab}	30.8^{ab}	0.3
Egg weight, g	65.4^{a}	65.9^{a}	66.5^{b}	68.1^{c}	65.9^{a}	0.2

[1)] ND - normal nutrient density, LD11 - 11 % lower nutrient density, LD21 - 21 % lower nutrient density, LD11^{OP} - 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

Fertilization and hatchability

The results of fertilized and hatched eggs (in %) are presented in Table 6 for the different treatments. Percentage of fertilized eggs was similar in different treatments. LD11^{OP} gave a significantly lower percentage of hatched eggs than ND, LD11 and LD12-ND.

Table 6. Effect of low-density diets on frequency of fertilized and hatched eggs in the period from week 25-60

Treatment[1)]	ND	LD11	LD21	LD11^{OP}	LD12-ND	SEM
% fertilized	93.4	93.3	93.3	92.6	93.5	0.2
% hatched	86.5^{b}	86.8^{b}	85.9^{ab}	84.3^{a}	86.9^{b}	0.3

[1)] ND - normal nutrient density, LD11 - 11 % lower nutrient density, LD21 - 21 % lower nutrient density, LD11^{OP} - 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

Egg composition and embryonic development

Results of egg content weights during incubation are given in Table 7. After 24 hours of incubation, egg content weights were similar in eggs from birds given ND and LD21. After 264 hours of incubation however, egg content weight in ND birds was significantly lower than in eggs of LD21 birds. This indicates a higher weight loss in eggs form birds given ND. LD21 gave significantly higher egg shell weights than ND in week 29 ($P<0.02$) and in week 41 ($P<0.05$) (results not given).

Eggs from LD21 given hens had a significantly higher white/yolk ratio at 29 and 41 weeks of age compared with hens on ND (Table 8). The difference in white/yolk ratios in eggs of hens of 29 weeks of age was larger than the difference in eggs produced by hens of 41 weeks of age. White/yolk ratios of eggs from 41 weeks-old hens were lower than of eggs from hens of 29 weeks of age ($P<0.01$).

Table 7. Weight of the egg contents of ND and LD21 in week 29 and 41 during different duration incubation (until 264 hrs)

Treatment[1]	Duration Incubation, hr	ND Egg content, g	SEM	LD21 Egg content, g	SEM	P
Week 29	24	51.33	0.61	51.68	0.78	<0.001
	36	49.84	0.79	51.23	0.80	
	48	50.25	0.62	51.72	0.79	
	72	49.46	0.56	51.51	0.64	
	264	48.65	0.54	49.53	0.50	
Week 41	24	59.65	0.63	59.52	0.74	<0.001
	36	58.29	0.67	59.46	0.66	
	48	58.46	0.49	59.38	0.69	
	72	57.99	0.58	59.10	0.51	
	264	56.29	0.49	56.96	0.46	

[1] ND - normal nutrient density, LD21 - 21 % lower nutrient density.

Table 8. White/yolk ratio of eggs of ND and LD21 in week 29 and 41 during the first 72 hours of incubation

Treatment[1]	Duration Incubation, hr	ND White/yolk Ratio	SEM	LD21 White/yolk Ratio	SEM	P
Week 29	24	1.707	0.030	1.775	0.059	<0.008
	36	1.690	0.037	1.756	0.044	
	48	1.626	0.043	1.801	0.055	
	72	1.646	0.044	1.679	0.052	
Week 41	24	1.594	0.029	1.612	0.022	<0.008
	36	1.480	0.020	1.543	0.030	
	48	1.485	0.023	1.532	0.027	
	72	1.287	0.025	1.299	0.029	

[1] ND - normal nutrient density, LD21 - 21 % lower nutrient density.

Table 9 presents the surface of the area vitellina externa during the early incubation process. Data on the area vasculosa surface are given in Table 10. Eggs from hens given LD21 showed a significantly larger area vitellina externa both at 29 and 41 weeks of age compared with eggs from hens given ND. The largest differences were observed in eggs layed at week 29. ND and LD21 gave a similar area vasculosa surface at 29 and 41 weeks of age.

At 29 weeks of age, LD21 gave significantly higher heart and embryo weights compared with ND (Table 11). No differences were observed between the eggs of hens of different treatments at 41 weeks of age. Heart and embryo weights were higher in eggs of broiler breeders of 41 weeks of age compared with 29 weeks of age.

Table 9. Surface area of the area vitellina externa of embryo's in eggs of ND and LD21 in week 29 and 41 during the first 48 hours of incubation

Treatment[1)]	Duration Incubation, hr	ND Surface area, mm^2	SEM	LD21 Surface area, mm^2	SEM	P
Week 29	24	58.5	4.9	83.3	6.1	< 0.001
	36	145.7	16.2	178.5	12.2	
	48	700.0	56.3	910.1	2.8	
Week 41	24	84.3	6.6	99.9	13.7	< 0.001
	36	383.1	25.5	473.3	29.7	
	48	837.1	44.9	858.4	37.3	

1) ND - normal nutrient density, LD21 - 21 % lower nutrient density.

Table 10. Surface area of the area vasculosa of embryo's in eggs of ND and LD21 in week 29 and 41 during the first 72 hours of incubation

Treatment[1)]	Duration Incubation, hr	ND Surface area. mm^2	SEM	LD21 Surface area. mm^2	SEM	P
Week 29	48	37.7	2.9	43.7	3.1	NS
	72	179.7	14.4	211.3	24.3	
Week 41	48	44.5	1.9	48.3	2.6	NS
	72	336.0	15.2	335.2	26.2	

1) ND - normal nutrient density, LD21 - 21 % lower nutrient density.

Table 11. Heart and embryo weights in eggs of ND and LD21 in week 29 and 41 after 264 hours of incubation

Treatment[1]	Duration Incubation, hr	ND Weight heart, mg	SEM	LD21 Weight heart, mg	SEM	P
Week 29	264	12.4	0.7	15.6	0.6	<0.001
Week 41	264	26.2	0.7	26.1	0.6	NS
		weight embryo, g		weight embryo, g		P
Week 29	264	1.67	0.05	2.04	0.06	<0.001
Week 41	264	3.26	0.07	3.24	0.06	NS

[1] ND - normal nutrient density, LD21 - 21 % lower nutrient density

Discussion

Low-density diets did not affect live weight of female birds during the laying period when palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal were used as components to lower the diet density. The use of oats and sugar beet pulp in the low-density diet ($LD11^{OP}$) however gave a significantly lower live weight, indicating that fibre type in oats and sugar beet pulp affects live weight. Enting et al. (submitted) found a lower than expected digestibility of the $LD11^{OP}$ diet.
Hens given LD11 showed a higher rate of lay compared with ND hens. A similar increase had been observed by Zuidhof et al. (1995) when broiler breeder diets were diluted with 15 % oat hulls. In our LD21 birds and in birds given diets diluted with 30 % oat hulls (Zuidhof et al.,1995), no increase in rate of lay was found. The higher nutritive value of LD11 because of a higher than expected digestibility and AME content (Enting et al., 2005) indicates that relatively small changes in feed allowance of broiler breeders affect performance. This was found by Fattori et al. (1990; 1993), Attia et al. (1995) and Robinson et al. (1998).
Low-density diets gave a significant increase in egg weight. The largest increase in egg weight was observed when hens were given $LD11^{OP}$. According to Al Bustany and Elwinger (1987), Shafer et al. (1996), Schutte et al. (1994) and Whitehead et al. (1993; 1996), amino acid and linoleic acid intake can have a strong effect on egg weight. Since $LD11^{OP}$ did not contain more digestible amino acids and linoleic acid than LD11, the increased egg weight can not to be related to this. In treatment LD12-ND, in which ND diets were given during the laying period in addition to LD11 during rearing, also an increase in egg weight was observed compared with birds given ND. In an earlier unpublished study (Smulders and Enting, 2000), no increase in egg weight was found when low-density diets were given during the laying period only. This indicates that feeding of low-density diets during the rearing period can affect egg weight. Enting et al. (2005) found a delay in the development of the reproductive tract when low-density diets were given during rearing, particularly when hens were given $LD11^{OP}$. The delay in development of the reproductive tract was also reflected in the higher age at which peak production was achieved on

LD11 and LD11^{OP}. In general, a delay in the onset of laying gives higher egg weights (Kwakkel et al., 1991; Hocking, 1996; Bruggeman et al., 1999). The results of this experiment indicate that low-density diets given during rearing increase egg weight, which is associated with a delay in reproductive tract development.

When birds were given LD11^{OP}, a significant lower hatchability was observed in comparison with the other treatments. Morris et al. (1969) and Szczerbinska and Zubrecki (1999) found a lower hatchability with increasing egg weights. Therefore, the lower hatchability of eggs of birds given LD11^{OP} might be the consequence of the higher egg weight, which can limit gas exchange during incubation.

Data of the incubation studies showed that the increased egg weight of hens on LD21 was due to an increase in egg white weight, giving a significantly higher white/yolk ratio. The differences between white/yolk ratio in eggs of hens given ND and LD21 can not be related to differences in intake of first limiting nutrients during the laying period. Therefore, the origin of the differences in white/yolk ratio probably has the same origin as the differences in egg weight. This indicates that differences in the development of the reproductive tract can affect egg composition.

The higher egg weight and white/yolk ratio in eggs of hens on LD21 related to a higher growth of the area vitellina externa and heart and embryo weights during incubation. The largest effects were observed in eggs from young broiler breeders. The higher weight of the egg itself did probably not directly cause the increased growth rate of the area vitellina externa and the embryo in eggs from birds given LD21, since Hassan and Nordskog (1971), Washburn and Guill (1974) and Al Murrani (1978) found no positive relationship between egg weight and embryo weight until day 14 of incubation. Shanawany (1984) observed that an increased flock age was related to a higher embryo development rate and embryo weight. This was also found in the present experiment and by Yannakopoulos and Tserveni-Gousi (1987), Applegate and Lilburn (1996) and Christensen et al. (1996) in quail and turkeys. Based on the differences between white/yolk ratio and embryonic development in eggs from hens given ND and LD21, it can be hypothesized that the amount of white in eggs of particularly young broiler breeder hens is a limiting factor in the development of the embryo. According to Noble et al. (1986a&b), Yaffei and Noble (1990) and Vajda et al. (1994), embryos from young broiler breeders suffer from a lowered lipid transfer from the yolk and also from a lower metabolism of these yolk lipids. Since the higher amount of white in eggs from hens given LD21 was associated with a better development of the area vitellina externa, it can be hypothesized that this might give a better yolk utilization. This can overcome negative effects in the development of embryos from young broiler breeders and indicates that low-density diets can be particularly beneficial for the development of chickens from hens at the beginning of the laying period. This might have further implications for broiler chicken development after hatching. However, since higher weight losses in eggs from hens given ND during incubation went together with a lower egg shell weight compared with eggs from hens on LD21, this also might have played a role in the observed differences in embryonic development (Peebles et al., 2001).

On the basis of the results from this study, it can be concluded that low-density diets can improve laying performance and increase egg weight. The increase in egg weight is due to an increase in the amount of egg white. Low-density diets improve embryonic development, which is associated with an increase in egg weight due to an increased amount of egg white.

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Chapter 6

The effect of low-density broiler breeder diets on performance and immune status of their offspring

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Abstract

Effects of low-density broiler breeder diets on offspring performance and mortality were studied using Cobb 500 breeders. Breeder treatments involved 4 experimental groups and a control group with normal density feeds (ND, 10.88 MJ AME/kg during rearing and 11.72 MJ AME/kg during laying). In LD11 and LD21 (treatment 2 and 3), nutrient density of the breeder feeds was decreased with 11 and 21 % respectively. This was achieved by inclusion of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal in the diets. Treatment 4 (LD11^{OP}) included a diet with an 11 % decreased nutrient density by the inclusion of oats and sugar beet pulp. In treatment 5, the same low density feed was given to the breeders as in treatment 2 during the rearing period, but was followed up by a normal density feed during the laying period (LD12-ND).

When breeders were 29, 41 and 60 weeks of age, eggs were collected, separated in a heavy and light weight class and offspring performance was recorded. Immune responses were determined in broiler chickens in three separate experiments. In these experiments, offspring was vaccinated at days 10 and 30 with 200 μg KLH-TNP per bird and titres against KLH-TNP were determined at 17 and 35 days of age.

On low-density diets, offspring showed an increased one-day-old chicken weight. As compared with offspring of breeders that received ND, the day 38 live weight of chickens from 29 week-old breeders given LD11 was significantly improved. Mortality was significantly reduced in offspring from 60 week-old parent stock given low-density feeds.

IgM titres in 35 day-old offspring from eggs with a lower than average weight were significantly reduced when 29 week-old broiler breeders were given low density diets. In offspring from eggs with a higher than average weight from 60 week-old parent stock given LD11 and LD21 diets, IgM titres were significantly higher compared with ND.

It was concluded that low-density broiler breeder diets can affect offspring growth rate, mortality and immune responses. An increase in offspring live weight was related to an increased egg weight and to a higher nutrient intake of breeders. The reduction in mortality rate and changes in immune responses might be related to an increase in egg weight and egg white to yolk ratio when feeding low-density breeder diets.

Introduction

Broiler chicken performance is highly dependent on the genetic potential of these birds (Havenstein et al., 1994). Besides genetic potential that originates from parent stock, breeder age, level of feed intake and dietary composition of breeder feeds may also influence offspring performance (Triyuwanta et al., 1992; Kidd et al., 1993; Lopez and Leeson, 1994; 1995; Hossain et al., 1998; and Peebles et al., 1998; 1999a;b).

Shanawany (1984), Yannakopoulos and Tserveni-Gousi (1987), Applegate and Lilburn (1996) and Christensen et al. (1996) observed a higher embryo development rate and embryo weight with increasing breeder age. Egg weight and yolk to egg white ratio increase with age (Fletcher et al., 1981; Al Bustany and Elwinger, 1987; MacGregor, 1979, as cited by Etches, 1996) and offspring performance of young broiler breeders (< 35 weeks of age) is generally less good than that of older broiler breeders of > 35 weeks of age (McNaughton et al, 1978; Lopez and Leeson, 1995; Peebles et al., 1999a).

Based on effects of breeder age on offspring performance, it can be hypothesized that an increase in egg weight and yolk to egg white ratio can improve embryonic development and broiler chicken performance. Enting et al. (2005b) observed an increase in egg weight and a better embryonic development in terms of an increase in area vitellina externa surface and higher embryo weight when young breeders were given low-density diets. Moreover, they found an increase in egg white to yolk ratio. These observed effects may raise the question to what extend these changes can improve offspring performance.

In addition to dietary composition, feed intake level of broiler breeders might also affect offspring performance. Broiler breeders are fed a restricted amount of feed to prevent health and reproductive disorders (Hocking et al., 1994). There are indications that current feed intake levels give hunger and chronic stress (De Jong et al., 2002; 2003). In humans, food shortage that results in hunger can result in retarded offspring development (Barker et al., 1995). Chronic stress during pregnancy has shown to increase mortality rate of offspring in rats (Lordi et al., 2000). Smulders and Enting (unpublished) observed a significant reduction in mortality rate of broiler chickens originating from breeders that were given low-density diets combined with an increased feed intake. Since Zuidhof et al. (1995) found indications for a reduction in chronic stress when broiler breeders were given diets that were diluted by oat hulls, it can be hypothesized that low-density diets can affect offspring mortality due to a reduced stress level in parent stock. Due to the immunosuppressive effect of stress hormones (Griffin, 1989), offspring immune status might be affected as well.

Based on the observation of Enting et al. (2005b) that low-density broiler breeder diets increased egg weight, egg white to yolk ratio and embryo weight and the possible effect of low-density diets on hunger and chronic stress in parent stock, offspring performance of breeders given diets with different nutrient densities was determined at different breeders ages.

Material and methods

The experimental protocols were in agreement with standards for experiments with animals. The experiments were approved by the Ethical Committee of Schothorst Feed Research.

Broiler breeder treatments

The broiler breeder experiment involved in total 2,700 Cobb 500 female birds during the rearing period and 2,100 Cobb 500 female and 210 Cobb 500 male breeders during the laying period. These birds were housed in 30 floor pens of 4.5 x 3 m with 90 female birds per pen during the rearing period. In the laying period, 70 female and 7 male birds were housed per pen. Male birds were obtained at 25 weeks of age from De Kuikenaer Opfok (Delden, The Netherlands).
The broiler breeders were subjected to 5 different treatments, in which each treatment included six replicates with replicate as block. Treatment 1 of the broiler breeders was the control group, in which normal density diets were given during the rearing and laying period (10.88 and 11.72 MJ AME/kg respectively, ND). In treatment 2 and 3, the level of energy, digestible lysine, calcium, retainable phosphorus, sodium and linoleic acid were decreased by 12 and 23 % in the rearing period and by 11 and 21 % in the laying period (LD11 and LD21). These nutrient densities were decreased by inclusion of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal in the diets. Treatment 4 included diets with the same nutrient density as in treatment 2, but in this treatment, the lower nutrient density was reached by the inclusion of oats and sugar beet pulp instead of palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal ($LD11^{OP}$). In a pilot study, Smulders and Enting (unpublished) observed no significant changes in egg weight and offspring mortality when low-density diets were only fed during the laying period. Therefore, treatment 5 included a diet with a 12 % lower nutrient density in the rearing period and a ND diet in the laying period (LD12-ND).
In treatments with low-density diets, feed allowance was increased with the same percentage as the AME content of the low-density diets was decreased as compared with ND. This was done in order to obtain the same intake of first limiting nutrients in all treatments.

Animals and housing broiler experiments

At 29, 41 and 60 weeks of broiler breeder age, eggs were collected per pen, weighed and separated in two weight classes with higher and lower than average egg weight of the particular pen by a commercial egg packing station (Frisian Egg, Drachten, The Netherlands). This resulted in 60 groups of hatching eggs (30 pens of broiler breeders x 2 egg weight classes per pen). After separation in weight classes, eggs were incubated per pen and per weight class by Animal Sciences Group, Lelystad, The Netherlands. Eggs were incubated at a constant egg shell temperature of 37.8 °C during the entire incubation period in Petersime equipment.
After hatching, broiler chickens were sexed and transported to Schothorst Feed Research, Lelystad, The Netherlands, where birds were weighed per pen and per weight class. Each experiment in which broiler chicken performance was determined, included a total of 6,800 birds. Birds were placed in 40 pens of 4.95 x

2.05 m with 85 male and 85 female birds per pen, giving 8 replicates per treatment with 4 replicates per egg weight class.
In all broiler chicken experiments, light was provided during 23 hours a day. Temperature started at 32 °C at day 0 and was gradually decreased to 20 °C from day 28 on. The vaccination programme followed the recommendations of De Kuikenaer, Wezep, The Netherlands. Feed and water were provided ad libitum. Wood shavings were used as bedding material.

Dietary treatments and feed composition

The composition and calculated contents of the broiler breeder diets are described by Enting et al. (2005a) for the rearing period and by Enting et al. (2005b) for the laying period. The broiler chickens were given the same starter, grower and finisher diets in all treatments of the experiments. Starter diets were provided from day 0-15, grower diets from day 15-30 and finisher diets from day 30-38. The diets had wheat, corn and soya bean meal as main ingredients. The starter diet contained 12.13 MJ AME and 202 g crude protein per kg. The grower and finisher diets contained 12.76 MJ AME and 193 g crude protein per kg. Diets were formulated according to recommendations used in Dutch practice (CVB, 2003). The diets did not contain an antibiotic, but half a percent of formic acid as anti microbial growth promoter. The starter diet contained 3 mg/kg halofuginone and the grower diets 60 mg/kg salinomycine as anticoccidium. All diets were milled through a 3.2 mm screen and were given as pellets with a diameter of 2.5 mm in the starter period and of 3.0 mm in de grower and finisher phase.

Measurements

Weight of the collected eggs was recorded per pen and per weight class. During incubation, the number of fertilized and hatched eggs was recorded for each group. In each broiler chicken experiment in the floor pens, live weight and feed intake of the birds was determined at days 0, 15, 29 and 38. During the antibody response experiments, live weight and feed intake were recorded at days 0, 14, 30 and 37. Mortality was recorded daily in all experiments.
Immunization experiments were carried out with a total of 200 female broiler chickens per experiment. Birds were placed in pens of 1.40 x 1.25 m with 10 birds per pen. Each treatment included 4 replicates per treatment with 2 replicates per egg weight class. At 10 and 30 days of age, broiler chickens in the vaccination experiments were vaccinated with 200 µg 2,4,6-trinitrophenyl-keyhole limpet hemocyanine (KLH-TNP) in 0.1 and 0.2 ml saline solution, respectively. In serum samples, IgG and IgM anti-TNP titres as a result of the immunizations with KLH-TNP were determined in an ELISA system using BSA-TNP as a coating and specific antibody conjugates for detection. Serum samples were stored at -20 °C until use.

Statistical analysis

Results of the broiler chicken experiments were analysed by analysis of variance (general linear models procedure of GenStat 7.1, GenStat Committee, 2003). The statistical model included block (replicate), treatment and egg weight class within treatment as factors. Parameters were tested for normal distributions before statistical analysis. Output data are given as means with standard errors of means. Significant differences between treatments were detected by a least significant differences procedure (Snedecor and Cochran, 1967). Differences between treatments were considered significant at $P \leq 0.05$.

Results

The percentages of fertilized and hatched eggs were not different between treatments (not shown). Eggs from the relatively high weight class led to higher one-day-old chicken weights than eggs from the relatively low weight class at all breeder ages (Table 1). Eggs from 29 week-old breeders fed LD21 and $LD11^{OP}$ had significantly higher weights compared with egg from 29 week-old breeders given ND. The weight of one-day-old chickens was significantly higher when breeders were fed $LD11^{OP}$ than when ND, LD21 en LD12-ND were given at this age. Significant differences were observed in weight of eggs of 29 week-old breeders given LD11, LD21 and $LD11^{OP}$ as compared with breeders fed ND. Also significant differences were observed in one-day-old chick weight when 41 week-old breeder were fed LD11, LD21, $LD11^{OP}$ and LD12-ND as compared with 41 week-old breeders given ND. In week 60, eggs from breeders given LD21 and $LD11^{OP}$ had a significantly higher weight than when ND was fed. One-day-old chicken weight was significantly lower when breeders were given LD12-ND instead of ND, LD11 or LD21 at this breeder age. Weight of one-day-old chickens of 60 week-old breeders given $LD11^{OP}$ was significantly higher as compared with that of other breeder treatments.

At 29 weeks of breeder age, offspring live weight at 15 and 30 days was significantly higher when breeders were given LD11 and $LD11^{OP}$ as compared with breeders fed ND (Table 2). At 38 days of age, live weight was significantly higher when breeders were given LD11 instead of ND. This difference in live weight was larger in offspring from eggs with a lower than average weight than in chickens from eggs with a higher than average weight (88 vs. 33 g). Feed intake from day 0-15 and 0-30 was significantly higher when breeders were given LD11, LD21, $LD11^{OP}$ and LD12-ND than when breeders were fed ND. From day 0-38, feed intake was significantly higher when breeders were given LD11, $LD11^{OP}$ and LD12-ND instead of ND.

Table 1. Hatching egg weight and weight of one-day-old chickens of 29, 41 and 60 week-old broiler breeders given diets with different nutrient densities

	Treatment broiler breeders[1]					Egg weight class		
	ND	LD11	LD21	$LD11^{OP}$	LD12-ND	Heavy	Light	SEM
Egg weight, g								
week 29	55.4^{a}	55.8^{a}	56.5^{b}	58.4^{c}	55.9^{ab}	59.3	53.3	0.4
week 41	67.0^{a}	68.1^{b}	68.0^{b}	69.1^{c}	67.3^{a}	71.4	64.3	0.4
week 60	71.4^{a}	71.8^{a}	72.6^{b}	73.4^{c}	71.8^{a}	75.8	68.4	0.5
Day-old chick weight, g								
week 29	35.9^{a}	36.6^{ab}	36.3^{a}	37.3^{b}	35.8^{a}	38.3	34.2	0.3
week 41	41.8^{a}	42.5^{b}	42.8^{b}	45.0^{d}	43.4^{c}	45.3	41.1	0.3
week 60	45.1^{b}	44.8^{b}	45.1^{b}	45.9^{c}	43.9^{a}	47.3	42.6	0.4

[1] ND - normal nutrient density, LD11 – 11 % lower nutrient density, LD21 – 21 % lower nutrient density, $LD11^{OP}$ – 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

At a breeder age of 41 weeks, offspring live weight at day 15 and feed intake from day 0-15 were significantly higher when $LD11^{OP}$ and LD12-ND were given to breeders than when breeders were fed ND. Both live weight and feed intake in 15 day-old chickens of breeders given $LD11^{OP}$ were significantly higher than chickens of breeders fed LD12-ND. From day 0-30, feed intake was significantly higher when breeders were given $LD11^{OP}$ instead of ND.

When broiler breeders were 60 weeks of age, live weight of 15 and 30 day-old chickens was significantly higher when breeders were fed LD21 as compared with breeders given ND. Feed intake from day 0-15 was significantly higher when breeders were given LD21, $LD11^{OP}$ and LD12-ND instead of ND. From day 0-30, feed intake was significantly higher when parents were fed LD11, LD21 and LD12-ND as compared with parents given ND. In broiler chickens of 60 week-old breeders, feed intake from day 0-38 was significantly higher when breeders were given LD21 and LD12-ND instead of ND.

No significant differences in mortality rate were observed between treatments in offspring from 29 and 41 week old broiler breeders (Table 3). At a breeder age of 60 weeks of age, a significantly lower mortality rate was found from day 0-15 and 0-38 when breeders were given LD21, $LD11^{OP}$ and LD12-ND as compared with breeders given ND. From day 0-30, mortality in offspring of breeders fed LD12-ND was significantly lower than in offspring of breeders given ND.

Table 2. Live weight and feed intake of offspring of 29, 41 and 60 week-old broiler breeders given diets with different nutrient densities

		Treatment broiler breeders[1]					Egg weight class		
	Day	ND	LD11	LD21	LD11[OP]	LD12-ND	Heavy	Light	SEM
Live weight, g									
week 29	0-15	463[a]	479[b]	476[ab]	482[b]	474[ab]	487	461	3
week 41	0-15	503[a]	512[ab]	507[ab]	531[c]	517[b]	526	501	3
week 60	0-15	559[a]	562[ab]	571[b]	564[ab]	567[ab]	575	553	2
week 29	0-30	1438[a]	1478[b]	1448[a]	1470[b]	1458[a]	1481	1430	6
week 41	0-30	1611[a]	1631[ab]	1619[a]	1658[b]	1622[ab]	1644	1612	6
week 60	0-30	1563[a]	1586[ab]	1603[b]	1576[ab]	1575[ab]	1602	2478	7
week 29	0-38	2125[a]	2185[b]	2131[a]	2152[ab]	2154[ab]	2183	2112	8
week 41	0-38	2336	2345	2332	2378	2347	2370	2322	9
week 60	0-38	2302	2307	2325	2331	2319	2347	2286	9
Feed intake, g									
week 29	0-15	530[a]	547[b]	545[b]	551[b]	543[b]	556	529	3
week 41	0-15	579[a]	592[ab]	587[ab]	618[c]	597[b]	606	584	3
week 60	0-15	637[a]	646[ab]	654[b]	650[b]	651[b]	659	635	2
week 29	0-30	2100[a]	2174[b]	2156[b]	2144[b]	2144[b]	2172	2098	9
week 41	0-30	2456	2540	2468	2452	2518	2526	2478	16
week 60	0-30	2348[a]	2380[b]	2425[b]	2317[a]	2422[b]	2427	2358	9
week 29	0-38	3479[a]	3623[b]	3559[a]	3575[b]	3576[b]	3601	3510	15
week 41	0-38	3952	3973	3949	4025	3992	4002	3947	16
week 60	0-38	3929[a]	3956[ab]	4002[b]	4000[ab]	4009[b]	4010	3932	12

[1] ND - normal nutrient density, LD11 – 11 % lower nutrient density, LD21 – 21 % lower nutrient density, LD11[OP] – 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

Table 3. Mortality of offspring (%) of 29, 41 and 60 week-old broiler breeders given diets with different nutrient densities

		Treatment broiler breeders[1]					Egg weight class		
	Day	ND	LD11	LD21	LD11[OP]	LD12-ND	Heavy	Light	SEM
week 29	0-15	1.03	0.59	1.03	1.03	1.40	1.01	1.30	0.16
week 41	0-15	1.33	0.95	1.25	0.74	0.81	1.05	0.76	0.12
week 60	0-15	2.95[b]	2.13[ab]	1.62[a]	1.62[a]	1.51[a]	2.18	1.72	0.17
week 29	0-30	2.36	1.75	2.43	2.20	2.28	2.11	2.70	0.22
week 41	0-30	2.22	1.69	2.14	1.54	1.68	1.86	1.64	0.15
week 60	0-30	4.39[b]	3.07[ab]	2.89[ab]	2.92[ab]	2.27[a]	3.14	2.96	0.21
week 29	0-38	3.31	2.77	3.24	3.53	2.65	3.05	3.53	0.26
week 41	0-38	2.96	2.94	3.46	2.28	1.97	2.82	2.50	0.22
week 60	0-38	5.40[b]	3.67[ab]	3.48[a]	3.51[ab]	3.02[a]	3.99	3.50	0.26

[1] ND - normal nutrient density, LD11 – 11 % lower nutrient density, LD21 – 21 % lower nutrient density, LD11[OP] – 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

IgG and IgM titres in broiler chickens that were 17 days of age showed no clear differences between any of the treatment groups of the breeders (not shown).
In broiler chickens from 29 week-old breeders, IgM titres were significantly lower in broiler chickens that originated from the light weight category of eggs from breeders fed LD21, LD11^{OP} and LD12-ND as compared with titres in broiler chickens from breeders given a normal density diet (ND). For the heavy egg weight category, no differences were observed (Table 4).
At a breeder age of 41 weeks, IgM titres in broiler chickens from breeders given LD12-ND were significantly lower than in broilers from egg with a higher than average weight form breeders given ND.
IgM titres in broiler chickens from the heavy egg weight class from 60 week-old breeders were significantly higher in broiler chickens from breeders given LD11 and LD21 as compared with titres in broiler chickens from breeders fed ND. In broiler chickens from egg with a lower than average weight, IgM titres were significantly higher than in broiler chickens from breeders fed LD11^{OP} instead of ND at a breeder age of 60 weeks.
In offspring from eggs with a lower than average weight from young, 29 week-old breeders, the IgG titres in broilers derived from breeders that received LD11^{OP} were significantly lower as compared with titres in broiler chickens from breeders given ND (Table 5). IgG titres were significantly higher in broiler chickens from 60 week-old breeders given LD21 instead of ND when broiler chickens originated from eggs with a higher than average weight.

Table 4. IgM-titres at day 35 of offspring of 29, 41 and 60 week-old broiler breeders given diets with different nutrient densities

IgM-titre, ^{2}log	Egg weight class	Treatment broiler breeders[1] ND	LD11	LD21	LD11^{OP}	LD12-ND	Mean
week 29	heavy	9.96	10.30	10.35	9.18	9.70	9.84
	light	10.80^b	10.06	9.67^a	8.52^a	9.27^a	9.73
week 41	heavy	8.76^b	8.45	7.94	8.15	7.16^a	8.09
	light	7.97	7.87	8.46	8.73	8.17	8.24
week 60	heavy	8.78^a	10.96^b	11.56^b	9.09	9.55	9.75
	light	9.25^a	9.46	9.53	10.78^b	8.33	9.33

[1] ND - normal nutrient density, LD11 – 11 % lower nutrient density, LD21 – 21 % lower nutrient density, LD11^{OP} – 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

Table 5. IgG-titres at day 35 of offspring of 29, 41 and 60 week-old broiler breeders given diets with different nutrient densities

IgG-titre, ^{2}log	Egg weight class	Treatment broiler breeders[1] ND	LD11	LD21	LD11^{OP}	LD12-ND	Mean
week 29	heavy	7,03	7,03	6,95	6,52	6,82	6,87
	light	6,92^b	6,78	7,13	5,59^a	6,60	6,57
week 41	heavy	5,21	5,23	4,42	5,69	4,69	4,98
	light	4,57	4,64	5,07	5,07	5,00	4,90
week 60	heavy	4,89^a	6,25	8,16^b	4,89	6,01	5,92
	light	5,27	5,39	4,99	5,73	4,45	5,07

[1] ND - normal nutrient density, LD11 – 11 % lower nutrient density, LD21 – 21 % lower nutrient density, LD11^{OP} – 11 % lower nutrient density with other feedstuffs, LD12-ND – 12 % lower nutrient density during the rearing period, followed by ND during the laying period.

Discussion

The present results indicate that low-density broiler breeder diets can affect offspring performance through changes in egg size and egg composition. The increased egg weights resulted in increased weights of one-day-old chickens. Significant differences in broiler weight between dietary broiler breeder treatments were still present at day 15 and at day 30 when breeders were given LD11 and LD11^{OP}, but had disappeared at day 38. When breeders were given LD11, the difference in live weight was still significant at day 38 in broiler chickens from 29 week-old broiler breeders.

According to Larbier (1973), Leclercq (1966) and Triyuwanta et al. (1992), an increased egg weight caused by increased dietary amino acid and linoleic acid levels or by an increased feed allowance, can improve offspring growth rate. Based on findings of Lopez and Leeson (1994; 1995), this might be particularly true for early broiler chicken growth. Since egg weight of breeders given LD11 was lower than that of breeders fed LD11^{OP}, other factors than egg weight seem to affect offspring performance too. Results of Leclercq (1966), Larbier (1973) and Triyuwanta et al. (1992) indicate that nutrient intake levels of parent stock per se might also play a role in offspring performance. Enting et al. (2005a) observed a higher than expected digestibility of the LD11 diet, which resulted in a higher daily nutrient intake in this treatment. According to Gardner and Young (1972) and Shafer et al. (1996), who found higher crude protein levels in eggs when dietary amino acid levels were increased, the higher digestible nutrient level in LD11 could have resulted in higher nutrient levels in eggs. This may have given the increased live weight of offspring when breeders received LD11. McDevitt et al. (2004) reported that broiler chickens of a fast growing strain had a higher ability to digest feed when their parents were given diets that were supplemented with a carbohydrate hydrolysing enzyme. This can have given a higher nutritional value of the breeder diet. The importance of nutrient intake levels of breeders and the transfer of these nutrients to eggs might also be illustrated by the fact that the largest improvement in live weight gain was observed in broiler chickens from eggs with a lower than average weight when breeders were given LD11 (88 vs. 33 g for broiler chickens from the high egg weight class).

Enting et al. (2005b) reported changes in egg weight, egg white/yolk ratio and embryonic development when breeders received LD21 diets. However, these changes did not result in increased final live weights of broiler chickens. Therefore, to obtain a high feed intake and growth rate in broiler chickens, changes in egg white/ratio and embryonic development might be of less importance than digestible nutrient intake levels in broiler breeders.

Dietary broiler breeder treatments did not affect mortality of offspring of 29 and 41 old broiler breeders, but low-density breeder diets gave a significant decrease in mortality rate of offspring of 60 week old breeders. At this breeder age, mortality in offspring of breeders given ND was higher than at 29 and 41 weeks of age. In an earlier performed study (Smulders and Enting, unpublished), a significant reduction in broiler mortality of respectively 3.3 and 2.7 % was observed with 26 and 40 week-old broiler breeders given the same low-density diets as in this study. The results of the latter and the present study indicate that low-density breeder diets can give a significant reduction in broiler chicken mortality. The results of the present study also indicate that feeding low-density diets during the rearing period of broiler breeders is essential is this. Results of the earlier performed study (Smulders and Enting, unpublished) also stress this, since no reduction in mortality was found when low-density feeds were only given during the laying period. It can be hypothesized that the importance of feeding low-density diets during the rearing period is related to changes in breeder and reproductive tract development, as was found by Enting et al. (2005a), and to changes in egg size and composition due to changes in reproductive tract development (Enting et al., 2005b). Lopez and Leeson (1994) observed a lower average mortality of male broiler chickens in the period from day 0-49 when the crude protein level of the breeder diet was increased from 90 to 111, 130 or 150 g/kg. These increases in crude protein level gave an increase in egg weight of 1.4 gram and an increase in one-day-old chick weight of 2.3 gram. These results indicate that a higher egg and one-day-old chick weight might have a positive effect on mortality rate. However, egg weight itself is not the only factor in this, since no differences in mortality could be observed between broiler chickens of the two egg weight classes in the present study.

The significant differences in IgG and IgM titres in broiler chickens of 35 days of age indicate that low-density breeder diets can affect humoral immune responses of offspring. No clear differences in IgG and IgM titres were observed at day 7 after the first KLH-TNP immunization at 10 days of age. It appeared therefore that effects of broiler breeder diets developed relatively late after hatching. However, immune responses in young broiler chickens are low and biological variation may not allow to

detect significant differences at that age (Praharaj et al., 1997).
Differences in humoral responses in broiler chickens were observed after a second immunization on day 30 of age. Primary responses (IgM) were significantly lower in broiler chickens from eggs with a lower than average weight of 29 weeks-old breeders given low density diets LD21, LD11^{OP} and LD12-ND instead of ND. This effect was not observed in broiler chickens from eggs with a higher than average weight at 29 weeks of breeder age.
In offspring of 41 week-old breeders, no effect of different diets was observed in broiler chickens from relatively light eggs. When breeders were given LD11 and LD21 instead of ND, a significant increase in IgM titres was found in offspring from egg with a higher than average weight. The results indicate that no clear differences in IgM response were observed in broiler chickens from egg weighing about 59 to 65 g. Lower egg weights from young broiler breeders led to reduced responses when low-density diets were given. Higher egg weights (> 68 g) gave higher IgM responses in broiler chickens derived from 60 week-old breeders. These results suggest that the limited amount of nutrients in eggs with a relatively low weight may be used for growth rather than for the preparation of the immune system of the young bird. The mechanism underlying this effect is not yet unravelled, but nevertheless this indicates that competition for vital functions may exist.
Differences in IgG titres were similar to those observed for IgM titres. However, significant differences were only found in broiler chickens from the lowest egg weight class of 29 week-old breeders given LD11^{OP} (reduced titres) and in chickens from the highest egg weight class of 60 week-old breeders given LD21 (increased titres). This indicates that the priority of the IgG response in broiler chickens is less sensitive to events early in live (Tizard, 1982).

Differences in IgM and IgG titres seem to be more related to differences in egg weight and egg composition than to differences in nutrient intake of the breeders, since broiler chickens of breeders given LD11 did not show the highest titres. De Jong et al. (2005) found no effects of low-density diets on corticosterone level and heterophil to lymphocyte ratio in 26 week-old broiler breeders. However, a significant increase in heterophil to lymphocyte ratio was observed at 40 weeks of age when breeders were given LD21 as compared with breeders given ND. Since significantly lower titres were observed in offspring of 29 week-old breeders given low-density diets and almost no differences in titres were found in offspring of 41 week-old breeders, no indications were found that stress levels in broiler breeders affected offspring immune responses.

Based on the results of these studies, it can be concluded that low-density broiler breeder diets can affect offspring growth rate, mortality and humoral immunity. Changes in offspring growth rate seem to be mainly related to differences in nutrient intake of parents. Differences in offspring mortality and humoral immunity might be related to differences in egg weight and egg composition.

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Chapter 7

General Discussion

Introduction

In order to increase profitability in the broiler meat production chain, broiler breeders have to produce a high number of hatching eggs that result in broiler chickens with a high growth potential and a low mortality rate. Due to a negative relationship between growth rate and reproductive performance in broiler breeders (Bruggeman, 1998; Renema et al., 1999), ad libitum feeding of these birds results in a low number of hatching eggs (Hocking et al., 1994). Therefore, broiler breeders are fed restrictedly to improve reproductive performance.

Besides negative effects of restricted feeding on hunger and chronic stress in broiler breeders, restricted feeding might also affect offspring performance. According to Applegate (2002), this might be related to an increased variability in early egg production and egg composition. Zuidhof et al. (1995) and Smulders and Enting (unpublished) found indications for a reduction in hunger and chronic stress when breeders were fed low-density diets. Moreover, Smulders and Enting (unpublished) observed a significant reduction in offspring mortality with these breeder diets. This might imply that a reduction in chronic stress levels in broiler breeders can reduce offspring mortality.

The main objectives of this thesis were to (1) investigate effects of low-density broiler breeders diets on changes in behaviour and stress physiology as indications for improved bird welfare, (2) to reproduce earlier observed effects on offspring performance and mortality and (3) to study possible explanations for changes in offspring performance and mortality.

Behavioural characteristics and stress physiology

There are different methods to measure indications for hunger, satiety and chronic stress in broiler breeders. Besides behavioural observations, plasma hormone and nutrient levels are used to indicate hunger and chronic stress (Savory and Maros, 1993; Hocking et al., 1993; 1996; Savory and Mann, 1997; De Jong et al., 2002). In Chapter 3, several methods, like behavioural studies and a feed intake motivation test, were used to find indications for reduced hunger and chronic stress when broiler breeders were given low-density diets. However, these methods gave conflicting results. During the rearing period, behavioural observations indicated that broiler breeders may benefit from low-density diets during the first half of the rearing period. Furthermore, low-density diets seemed to increase satiety on the basis of the feed intake motivation test. In contrast to this, plasma corticosterone and heterophil to lymphocyte ratio did not indicate differences in stress levels on different diets. Moreover, one could conclude that low-density diets impair broiler breeder welfare when significant reductions in plasma NEFA levels and glucose to NEFA ratios on these diets were taken into account. However, these reductions might be related to differences in feed passage rate. These results indicate that several measurements should be included in experiments to detect possible effects of diet composition on changes in hunger and chronic stress.

Differences in behaviour between diets disappeared in the second half of the rearing period in which feed intake levels were below 50 % of ad libitum feed intake (Chapter 3 and 4). According to De Jong et al. (2003), blood plasma corticosterone levels strongly increase below this feed intake level. It can be hypothesized that stress levels are that high at these levels of restriction, that it is difficult to discriminate between dietary treatments that can also affect stress levels, but to a lesser extend as the amount of feed given. Therefore, a higher feeding level combined with low-density diets might gave a more clear response on satiety and chronic stress during the second half of the rearing period. However, this higher feeding level might have a negative effect on reproductive performance (Bruggeman et al., 1999).

The feed intake motivation test used in Chapter 3 resulted in significant differences in compensatory feed intake between dietary treatments. These differences were not reflected in differences in behaviour in restricted fed birds at the same time. The reason for this discrepancy may be that diets were offered ad libitum in the feed intake motivation test, whereas feed intake was restricted in the rearing experiment. Differences in bulk capacity might therefore not have been detected by birds at a low feed intake level as applied during the rearing period. The results of the feed intake motivation test and the disappearance of differences in behaviour between diets at the highest level of feed restriction, both indicate that low-density diets may be more beneficial at less severe levels of feed restriction.

The results of the digestibility study showed that feed passage rate increased with low-density diets at a low feed intake level (Chapter 4). Although diets were calculated to provide the same total starch intake in all treatments, significant lower glucose and NEFA plasma levels were found on low-density diets (Chapter 3). This might be due to the higher feed passage rate on the low-density diets. Also differences in digestibility rate of feedstuffs used in the low density diets or negative effects of some feedstuffs on digestibility of other feedstuffs might have contributed to differences in blood glucose and NEFA levels. Since changes in blood glucose and NEFA levels on low-density diets resembled changes observed at higher levels of feed restriction, the potential effect of low-density diets on satiety might have been counteracted by changes in blood glucose and NEFA levels. Current knowledge on absorption kinetics of feedstuffs and bulk capacity in the gastrointestinal tract is not sufficient to predict possible effects of (low-density) diets on satiety in broiler breeders. Also information on effects of absorption kinetics on satiety itself is limited in poultry, which hampers improvement of satiety by dietary manipulation.

Growth development and reproductive performance

An increased growth rate due to an increase in feed intake results in an earlier development of the reproductive tract and in a reduction in the number of hatching eggs (Katanbaf et al., 1986; Hocking et al., 1994; Renema et al., 1998; Bruggeman et al., 1999; Hocking and Robertson, 2000). The delay in ovarium and oviduct development that was observed when low-density diets were given, resembled that of the delay after more severe feed restriction during rearing (Chapter 4). Changes in reproductive tract development were related to differences in nutrient digestibility, feed passage rate and utilization of absorbed nutrients. During the laying period, a significant increase in rate of lay was found when the low-density diet had a better than expected digestibility (Chapter 5). Since low-density diets were optimized to give the same digestible energy and nutrient intake levels as the normal density diets, current knowledge of effects of diet composition on feed passage rate and nutrient digestibility is not sufficient to predict the effect of these factors on broiler breeder development.
The delay in reproductive tract development between 24 and 26 weeks of age when low-density diets were given (Chapter 4) was reflected in an increased egg weight during the entire laying period (Chapter 5). Correlations of 0.81 and 0.86 between egg weight and changes in ovarium and oviduct weights were calculated respectively. This indicates a strong carry-over effect from the rearing to the laying period, which was also found by Smulders and Enting (unpublished). Furthermore, this suggests a direct relationship between the development of the reproductive tract and egg size. Since the increase in egg size was due to an increased amount of egg white (Chapter 5), this also suggests a direct relationship between reproductive tract development and egg composition. Bruggeman (1998) observed differences in reproductive performance when feed intake was restricted in different phases of the rearing period, which was related to changed levels in reproductive hormones. Results given in Chapter 4 indicate that not only the amount of feed, but also the dietary composition is essential for reproductive performance. It is not clear yet to what extend this is mediated by changed levels of reproductive hormones.

Egg composition and embryonic development

The development of chicken embryos is dependent on the amount of nutrients in the egg, the ability to use these nutrient and on the incubation conditions. Larger egg weights are related to heavier one day-old chickens (Chapter 6; Triyuwanta et al., 1992; Tona et al., 2004b), indicating that embryos can effectively utilize the extra amount of egg white and yolk in larger eggs. It can be questioned if egg weight itself or the separate amounts of egg white and yolk are important for embryonic development. Most work in this field has been focussed on the effect of age on egg size and egg composition and hence on embryonic development (Chapter 5). This makes it difficult to make a distinction between specific effects of age and of egg size and egg composition.

Studies in which part of the egg white was removed or with double yolked eggs have shown that both egg white and yolk are important for embryonic development (Miyoshi and Mitsumoto, 1995; Burke et al.,1997). The results obtained with low-density diets indicate that egg weight and the amount of egg white are important factors for embryonic development.

In Chapter 5, it was hypothesized that larger amounts of egg white, that gave a better development of the area vitellina externa, can improve yolk utilization due to an increased absorption surface. The question remains whether a better developed area vitellina externa results in a better developed intestinal tract of broiler chickens. If the latter would be true, this might result in a better digestion or absorption of nutrients or in a better immune status of the intestinal tract. According to Uni (2003), a better intestinal tract development may have a positive effect on early broiler chicken growth and disease resistance.

Offspring performance

A number of studies have focussed on effects of breed, selection line, egg storage and incubation conditions on day-old chick quality and weight and on subsequent effects of performance (Christensen et al., 2001; Lourens, 2001; Peebles et al., 2001; Tona et al., 2003; 2004a; 2005). When differences due to sex, broiler breeder age and different incubation conditions were accounted for, most studies did not show any relationship between one day-old chicken weight and weight at slaughter (McLoughin and Gous, 1999; Tona et al., 2004b). In the experiments described in Chapter 6, also no clear relationships were found between the weight of day-old chickens and slaughter weight. However, an increase in digestible nutrient intake in broiler breeders resulted in a higher offspring weight at slaughter. This might be related to higher nutrient levels in eggs, as was found for a number of nutrients in studies with laying hens (Al Bustany and Elwinger; Shafer et al., 1996). The importance of nutrient levels in eggs might be emphasized by the fact that differences in live weight gain of broiler chickens were more pronounced when chickens originated from eggs with a lower than average weight compared to eggs with a higher than average weight (Chapter 6). A further illustration of the importance of nutrient levels in eggs on the growth rate of broiler chickens might be given by studies in which nutrients were injected into eggs. Larbier (1973), Ohta et al. (1999) and Uni (2003) showed that this can give a significant increase in broiler chicken live weight. Since highly concentrated pre-starter diets for broiler chickens can increase initial growth and weight at slaughter (Wijtten et al., 2004), it seems that increased nutrient levels in eggs may result in comparable effects. This might be nutrient dependent, since increased egg weights and one day-old chicken weights do not have to result in increased slaughter weights.

Tona et al. (2003) concluded that some unknown intrinsic factors may be involved in effects of broiler breeder age and length of egg storage on broiler growth and post-hatch production quality. They suggested that these factors might include factors present in the breeder that are transferred into the egg or into other factors in the developing embryo. The results given Chapters 4 to 6 indicate that nutrient intake of broiler breeders prior to and in the beginning of the laying period might be such an unknown factor as mentioned by Tona et al. (2003). However, information about effects of nutrient intake levels in broiler breeders, subsequent carry over of these nutrients to eggs and effects on offspring performance is very limited and needs further attention.

There is very limited evidence that broiler breeder diets can affect offspring mortality (Lopez and Leeson, 1994; Hossein et al., 1998). However, results from the pilot and the current study show that low-density diets can effectively reduce offspring mortality. Since the reduction in mortality was not concentrated in the first or last weeks of the growing period, it seems that low-density breeder diets give a more vital chicken in general. In addition to this, there might also be a more specific effect of low-density diets on offspring vitality.
Low-density breeders diets resulted in an increase in egg weight due to a higher amount of egg white. According to Butts and Cunningham (1972), the composition of egg white is rather constant with increased amounts of egg white. Therefore, an increased amount of egg white can result in a higher amount of egg white proteins in the egg. Since IgM is one of these proteins, this might indicate that the amount of IgM increases with an increased amount of egg white. IgM in egg white is mainly absorbed by the intestinal tract in the developing embryo (Tizard, 1982). In this way, an increased amount of egg white and IgM in the egg might result in a better development of the intestinal immune system due to low-density breeder diets. Indications that might support this hypothesis were obtained by Rebel (unpublished data Animal Sciences Group, Wageningen University, Lelystad, The Netherlands). In a study performed with male offspring of 40-week old broiler breeders given diets with different densities (Chapter 5), smaller differences in spleen weights between infected and uninfected broiler chickens when their parents received low-density diets instead of normal density diets (Table 1). However, there are no other studies available to support this hypothesis.

Practical implications of low-density diets

Based on the results presented in this thesis, the practical use of low-density diets to improve broiler breeder welfare is limited to the first half of the rearing period. As was shown in the feed intake motivation test, low-density diets seem to increase satiety when fed ad libitum. This can indicate that low-density diets will have a more substantial contribution to the improvement of bird welfare at higher feed intake levels as compared with the ad libitum feed intake. A further reduction in nutrient levels in low-density diets might also give a more substantial improvement of broiler breeder welfare. However, this further reduction will increase feed costs during the rearing period, which might hamper introduction of these diets in practice.

Low-density diets can be used to reduce mortality of offspring, in particular when average mortality rate is 5 % or higher. In order to obtain a reduction in mortality, feeding low-density diets during only the rearing period will do. The AME content of the diets has to be decreased by 10-15 % as compared with normal density diets (10.9 MJ/kg). In addition to this, the amounts of first limiting nutrients have to be decreased with the same percentage as the AME content in these diets.

Low-density diets can be used to increase rate of lay. Therefore, diets with a 10-15 % reduced AME level are required in both the rearing and laying period as compared with normal-density diets (10.9 and 11.7 MJ/kg respectively). Also the amounts of first limiting nutrients have to be decreased with this percentge. Since these low-density diets gave an increase in digestible nutrient intake of about 4 % in comparison with normal-density diets, an increase in feed intake of about 4 % might also result in an increased rate of lay. *It is advised to use palm kernel meal, wheat bran, wheat gluten* feed and sunflower seed meal in order to obtain low-density diets instead of oats of sugar beet pulp, since the latter feedstuffs had a negative effect on litter quality at relatively high feed intake levels (results not shown).

Table 1. Effect of low density broiler breeder diets on average live weight and spleen weight with standard deviations of male broiler chickens from 41 weeks-old broiler breeders with and without malabsorption infection

	Chickens without malabsorption				Chickens with malabsorption			
Broiler breeder diet[1]	ND	LD11	LD21	LD11^{OP}	ND	LD11	LD21	LD11^{OP}
Day 10								
live weight, g	259	264	282	280	163	163	165	174
	± 19	± 1	± 0	± 8	±3	± 2	± 3	± 4
spleen weight, g	0.287	0.237	0.234	0.236	0.175	0.194	0.225	0.216
	± 0.062	± 0.068	± 0.043	± 0.055	± 0.081	± 0.069	± 0.041	± 0.061
Day 17								
live weight, g	643	644	667	683	457	461	446	482
	± 42	± 3	± 7	± 9	± 6	± 7	± 1	± 6
spleen weight, g	0.706	0.753	0.581	0.747	0.536	0.793	0.824	0.811
	± 0.241	± 0.226	± 0.234	± 0.154	± 0.190	± 0.212	± 0.301	± 0.207
Day 31								
live weight, g	2029	2013	2045	2091	1653	1655	1672	1743
	± 66	± 3	± 44	± 34	± 9	± 31	± 1	± 16
spleen weight, g	2.885	2.445	2.229	2.714	1.806	2.021	2.190	2.691
	± 0.764	± 0.257	± 0.389	± 0.514	± 0.353	± 0.253	± 0.361	± 0.951

[1] ND - normal nutrient density, LD11 - 11 % lower nutrient density, LD21 - 21 % lower nutrient density, LD11^{OP} - 11 % lower nutrient density with other feedstuffs.

Summarizing conclusions

On the basis of the experiments described in this thesis, a number of conclusions can be drawn. It can be stated that low-density broiler breeder diets:

- can give a reduction in object pecking and increase the percentage of time spent on sitting during the first half of the rearing period. This indicates an improved bird welfare. When fed ad libitum, feed intake motivation is decreased on low-density diets, indicating an increase in satiety (Chapter 3).
- give a large increase in feed consumption time and can increase heterophil to lymphocyte ratio during the laying period. This indicates an impaired bird welfare (Chapter 3).
- delay ovary and oviduct development and, as a consequence, increased subsequent egg weights. The increase in egg weight is due to an increased amount of egg white. The delay in ovary and oviduct development seems to be related to a reduced nutrient digestibility and utilization of digested nutrients (Chapters 4 and 5).
- can increase laying rate due to higher intake of digestible nutrients (Chapter 5).
- improve the early development of the area vitellina externa and increase embryo weight. This is related to the increase in egg and egg white weight (Chapter 5).
- can increase growth rate of offspring due to a higher intake of digestible nutrients of their parents (Chapter 6).
- can reduce mortality rate of offspring, also when low-density diets are only given during the rearing period. This is related to increased egg and egg white weights and not to changes in stress physiology during the rearing period (Chapter 6).
- decreased IgM and IgG titres in offspring from relatively light eggs from 29 week-old broiler breeders and increased these titres in offspring from relatively heavy eggs from 60 week-old broiler breeders. It seems that nutrients in eggs with a relatively low weight are used for growth rather than for the development of the immune system (Chapter 6).

The effects of low-density diets are summarized in Figure 1.

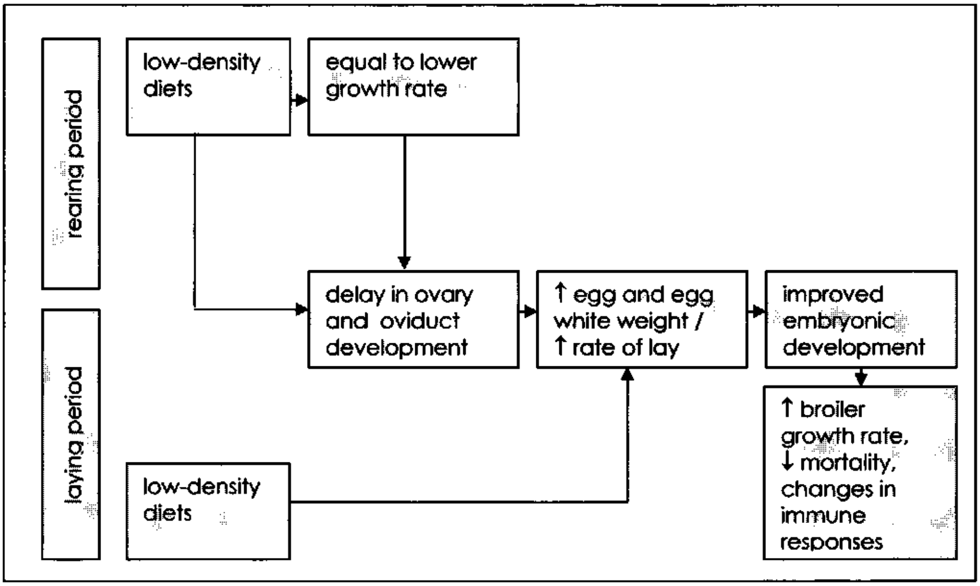

Figure 1. Relationships between broiler breeder nutrition during rearing and laying and offspring performance.

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Summary

Introduction

Broiler breeders are reared to produce a high number of hatching eggs, which yield broiler chickens with a high growth potential and a low mortality rate. Since broiler chicken parent stock is selected to transfer a high genetic growth potential to their offspring, broiler breeders also have a high growth potential. When broiler breeders are fed ad libitum, a high growth and fat deposition rate are obtained during the rearing period. Subsequently, laying performance is impaired. This impaired reproductive performance is related to a lower LH concentration in blood plasma and to a lower LH to FSH ratio when broiler breeders are fed ad libitum. In order to reduce live weight and fat deposition during the rearing period and to improve reproductive performance, restriction of feed intake has been successfully applied. However, current feed restriction levels can result in hunger feeling and chronic stress, particularly during the rearing period. Selection for a high growth rate has not only resulted in an impaired reproductive performance, but also is also associated with an increased variation in egg composition and an impaired performance of offspring of young broiler breeders.
The problem that has to be resolved is to reduce hunger feeling and chronic stress in broiler breeders without negative effects on reproductive performance. Based on literature data presented in Chapter 2, feeding of low-density diets at a higher feeding level could be one of the ways to improve breeder welfare due to an increase in the amount of bulk in the digestive tract.
Recent findings indicate that low-density breeder diets can also reduce mortality rate of their offspring. In literature, some indications are found for an improved offspring performance by dietary means. These indications are summarized in Chapter 2. It was hypothesized that this reduction in mortality rate could be related to reduced hunger and chronic stress levels in parent stock. Moreover, it was hypothesized that also changes in egg size and composition might explain the lower mortality rate.
The aim of the study described in this thesis was to evaluate the effect of low-density diets on welfare and reproductive performance of broiler breeders and on the performance and vitality of their offspring. Breeder diets with 3 different nutrient densities were tested during both the rearing and the laying period: normal density, ND (10.88 MJ/kg during the rearing period and 11.72 MJ/kg during the laying period); 12 and 23 % lower nutrient densities during the rearing period (LD12 and LD23) and 11 and 21 % lower nutrient densities during the laying period (LD11 and LD21). Feedstuff and fibre type effects were studied by replacing palm kernel meal, wheat bran, wheat gluten feed and sunflower seed meal in LD12 and LD11 diets by oats and sugar beet pulp ($LD12^{OP}$ and $LD11^{OP}$). Feeding of low-density diets during the rearing period followed by a normal density diet during the laying period was applied to study age effects of low-density diets (LD12-ND).
In all low-density diets, levels of the first limiting nutrients digestible lysine, calcium, retainable phosphorus and linoleic acid were lowered to the same ratio as the energy level. Daily intake of these nutrients was kept constant in all treatments by

increasing the amount of feed given with the same percentage as the energy level was lowered in treatments with low-density diets.

Effect of low-density diets on broiler breeder welfare

During both the rearing and the laying period of the broiler breeders, behavioural and physiological parameters were measured at different ages as indicators of hunger and frustration of feed intake motivation (Chapter 3). Low-density diets gave an increase in feed consumption time, particularly during the laying period. At 6 and 10 weeks of age, LD23 diets resulted in a significant reduction in stereotypic object pecking. Furthermore, time spent on sitting was significantly increased in LD23 at these ages. At 16 and 20 weeks of age, no effects of diets on behaviour were detected. Compensatory feed intake on LD23 and $LD12^{OP}$ diets at 12 weeks of age was significantly reduced. The reduction was significantly higher on $LD12^{OP}$ compared to LD12, indicating that not only nutrient density, but also fibre type or feedstuff type has an effect on compensatory feed intake. No differences in corticosteroid and heterophil to lymphocyte ratio were observed during the rearing period. Glucose to NEFA ratios were significantly increased at 10 and 26 weeks of age in LD23 birds. The results obtained during the rearing period indicated a reduction in hunger and frustration on LD23 during the first half of the rearing period. Moreover, the results of the feed intake motivation test indicated an increase in satiety in birds given LD23 and $LD12^{OP}$ diets. It should be noted that diets were given ad libitum in the feed intake motivation test.
During the laying period, LD11, LD21 and $LD11^{OP}$ diets gave a significant increase in feeding behaviour at the expense of time spent on sitting in LD11 and LD21. Heterophil to lymphocyte ratios were significantly increased in LD21 at 40 weeks of age. This indicated an increase in stress level in these birds compared with hen on other diets. This could be associated with the long feed consumption time on this diet. Thus, LD21 diets do not improve bird welfare during the laying period.

Effect of low-density diets on broiler breeder development and nutrient digestibility

Chapter 4 describes the development of broiler breeders during the rearing period and gives the nutrient digestibility of diets used in the broiler breeder experiment. Feeding $LD12^{OP}$ diets resulted in significantly lower live weights at the end of the rearing period. This was related to the lower nutrient digestibility of $LD12^{OP}$ diets than was expected. LD23 and $LD12^{OP}$ diets gave lower ovarium and oviduct weights compared with ND at 24 weeks of age. This was followed by a significantly faster ovarium and oviduct development between 24 and 26 weeks of age. Differences in bird and reproductive tract development between treatments were related to differences in nutrient digestibility and utilization of digested nutrients between diets.

Birds on different diets had similar gut contents. This indicates that changes in behaviour on low-density diets were not related to differences in satiety due to changes in digestive tract contents.

Effect of low-density diets on reproductive performance

Effects of low-density diets on laying performance, egg composition and embryonic development are given in Chapter 5. It was hypothesized that changes in reproductive tract development at the end of the rearing period would affect reproductive performance. As in the rearing period, LD11^{OP} diets gave significantly lower breeder weights during the laying period compared with the other diets included in our study. LD11 diets resulted in a significantly increased laying percentage compared with ND. Egg weights were significantly increased when low-density diets were given during both the rearing and laying period or during the rearing period only. Increased egg weights were related to changes in reproductive tract development at the end of the rearing period.
Low-density diets also influenced egg composition and embryonic development. The observed increase in egg weight was completely due to an increase in egg white weight. LD21 gave a significantly better development of the area vitellina externa and heart and embryo weights in eggs of 29-week-old breeders. The better embryonic development was associated with the increased egg weight and the amount of egg white. Differences in eggshell quality, which might explain a higher moisture loss during incubation in ND compared with LD21, could also have played a role in embryonic development.

Effect of low-density diets on offspring performance

Due to the observed effects of low-density diets on egg size, egg composition and embryonic development, it was hypothesized that these changes would affect offspring performance. At 29, 41 and 60 weeks of breeder age, eggs were collected, separated in a heavy and light weight class, hatched and performance and immune responses of offspring were recorded. Humoral immune responses were determined in three separate experiments with female broiler chickens at these breeder ages. Results of offspring experiments are reported in Chapter 6.
Low-density breeder diets gave a significant increase in day-old chickens weights. At 38 days of age, live weight in offspring of LD11 of 29-week-old breeders was significantly improved compared with that in other treatments. This increased live weight was strongest in offspring of eggs from the light egg weight class. Differences in offspring live weight were associated with differences in egg weight and in digestible nutrient intake of breeders.
Low-density diets given during both the rearing and laying period or during the rearing period only, gave a significant reduction in offspring of 60-week-old breeders. This was also observed when low-density diets were given during the rearing period

only. In offspring of 29 and 41 week old broiler breeders, no reduction in mortality was observed, but average mortality was low in offspring at these breeder ages.
IgM titres were significantly lower in offspring of eggs from the low weight class of 29 weeks old breeders given low-density diets. In offspring of eggs from the high weight class of 60 weeks old breeders, IgM titres were significantly higher in LD11 and LD21 compared with ND. The changes in offspring mortality and humoral immune responses were associated with changes in egg weight and egg composition when broiler breeders were given low-density diets.

Conclusions

Summarizing the results described in this thesis, the following conclusions can be drawn. Low-density broiler breeder diets:

- can give a reduction in object pecking and increase the percentage of time spent on sitting during the first half of the rearing period when nutrient density is decreased more than 20 %. This indicates an improved bird welfare. When fed ad libitum, feed intake motivation is decreased on low-density diets, indicating an increase in satiety. This effect is dependent on the feedstuffs included in the diet. Low-density diets do not increase intestinal tract contents due to a reduced mean retention time.
- give a large increase in feed consumption time and can increase heterophil to lymphocyte ratio during the laying period when nutrient density is reduced by more than 20 %. This indicates an impaired bird welfare.
- can delay ovary and oviduct development and, as a consequence, increase subsequent egg weights. The increase in egg weight is due to an increased amount of egg white. The delay in ovary and oviduct development seems to be related to a reduced nutrient digestibility and utilization of digested nutrients.
- can increase laying rate due to higher intake of digestible nutrients when nutrient density is decreased by about 12 %.
- improve the early development of the area vitellina externa and increase embryo weight. This is related to the increase in egg and egg white weight.
- can increase growth rate of offspring due to a higher intake of digestible nutrients of their parents when nutrient density is decreased by about 12 %.
- can reduce mortality rate of offspring, also when low-density diets are only given during the rearing period. This is related to increased egg and egg white weights and not to changes in stress physiology during the rearing period. The nutrient density of the diets has to be decreased by about 12 % or more.
- decreased IgM and IgG titres in offspring from relatively light eggs from 29 week-old broiler breeders and increased these titres in offspring from relatively heavy eggs from 60 week-old broiler breeders. It seems that nutrients in eggs with a relatively low weight are used for growth rather than for the development of the immune system.

Samenvatting

Inleiding

Voor het behalen van goede economische resultaten in de pluimveevleesketen, is het belangrijk dat vleeskuikenouderdieren veel broedeieren produceren, waaruit kuikens komen met een hoge groeisnelheid en een goede vitaliteit. Aangezien uitval en gebruik van antibiotica bij vleeskuikens wordt geassocieerd met hun hoge groeisnelheid, vormt de vitaliteit van de kuikens eveneens een belangrijk aandachtspunt in de pluimveevleesketen naast een hoge broedeiproductie en een hoge groeisnelheid.
De ouders van vleeskuikens worden geselecteerd op een hoge groeisnelheid, zodat zij deze eigenschappen kunnen doorgeven aan de volgende generaties en uiteindelijk aan de vleeskuikens. Dit betekent dat de ouders van vleeskuikens, de vleeskuikenouderdieren, ook een hoge groeisnelheid kunnen realiseren. Bij het onbeperkt voeren van de ouderdieren bereiken zij dan ook een hoog lichaamsgewicht aan het eind van de opfokperiode, waarbij veel vet wordt aangezet. Onbeperkt gevoerde vleeskuikenouderdieren blijken weinig broedeieren te produceren. Dit is het gevolg van een lagere LH concentratie en een lagere LH/FSH-verhouding in het bloed. Deze hormonen zijn van belang bij het op gang komen en reguleren van de eiproductie. Wanneer ouderdieren beperkt worden gevoerd tijdens de opfokperiode, neemt de LH concentratie en de verhouding tussen LH en FSH toe. Beperkt gevoerde ouderdieren produceren hierdoor meer broedeieren dan onbeperkt gevoerde ouderdieren.
Het huidige niveau van voerbeperking tijdens de opfokperiode van ouderdieren is echter in vergelijking met de onbeperkte voeropname dermate hoog, dat dit hongergevoel kan geven. Daarnaast worden de hoge groeisnelheid van de ouders van vleeskuikens en een minder goede broedeiproductie bij een hoge groeisnelheid ook in verband gebracht met een toename van de variatie in eisamenstelling en met minder goede prestaties en een hoger uitvalspercentage van met name kuikens van jonge ouderdieren. Vanuit het dierenwelzijn is het gewenst het hongergevoel bij de ouderdieren te verminderen en de vitaliteit van vleeskuikens te verbeteren. Het onderzoek dat in dit proefschrift is beschreven richt zich hier op.
Een belangrijke vraag in het onderzoek is in hoeverre het mogelijk is het hongergevoel bij vleeskuikenouderdieren te verminderen zonder dat dit ten koste gaat van de broedeiproductie. In hoofdstuk 2 wordt op deze mogelijkheden ingegaan. Van de voedingstechnische maatregelen zou het verstrekken van minder geconcentreerde voeders, waarbij de voergift wordt verhoogd, een mogelijkheid kunnen zijn. Het verstrekken van dergelijke voeders zou een hogere vulling van het maagdarmkanaal kunnen geven, waardoor het verzadigingsgevoel kan toenemen.
Resultaten van recent uitgevoerd onderzoek geven aan dat voeders voor vleeskuikenouderdieren met een 12-25 % lagere nutriëntendichtheid een 30-40 % lager uitvalspercentage van de kuikens van deze ouderdieren kunnen geven. Mogelijk is dit het gevolg van een afname van hongergevoel en chronische stress bij de ouderdieren wanneer deze voeders worden verstrekt, maar ook veranderingen in

eigrootte en eisamenstelling zouden hierbij een rol kunnen spelen (hoofdstuk 2).
In de proeven, die in dit proefschrift zijn beschreven, werd nagegaan in hoeverre minder geconcentreerde voeders invloed hebben op het welzijn en reproductiekenmerken van vleeskuikenouderdieren. Daarnaast werd nagegaan in hoeverre minder geconcentreerde ouderdierenvoeders invloed hebben op de ontwikkeling en de vitaliteit van de kuikens van deze ouderdieren. In het onderzoek werden tijdens zowel de opfok- als de legperiode ouderdierenvoeders met 3 verschillende nutriëntenniveaus getest, waarbij de voergift met hetzelfde percentage werd verhoogd als de nutriëntengehalten werden verlaagd: normale nutriëntengehalten, ND (10,88 MJ/kg tijdens de opfokperiode en 11,72 MJ/kg tijdens de legperiode), voeders met 12 en 11 % lagere nutriëntengehalten tijdens de opfok- en legperiode (LD12 en LD11) en voeders met 23 en 21 % lagere nutriëntengehalten tijdens de opfok- en legperiode (LD23 en LD21). Daarnaast werd de invloed van grondstoffen en het type vezels in de voeders bij het verlagen van het nutriëntengehalte in het voer bestudeerd door palmpitschilfers, tarwegries, tarweglutenvoer en zonnebloemzaadschroot in de LD12 en LD11 voeders uit te wisselen tegen haver en bietenpulp ($LD12^{OP}$ en $LD11^{OP}$). Verder werd een minder geconcentreerd voer tijdens de opfokperiode gecombineerd met een voer met een normaal nutriëntengehalte tijdens de legperiode (LD12-ND). Hiermee kon de invloed van de leeftijd, waarop minder geconcentreerde voeders werden verstrekt, op de ontwikkeling en de vitaliteit van de kuikens worden bestudeerd. In de minder geconcentreerde voeders was het gehalte van de eerst limiterende nutriënten (verteerbaar lysine, calcium, opneembaar fosfor en linolzuur) met hetzelfde percentage verlaagd als het OE-gehalte. Hierdoor werd de dagelijks opname van deze nutriënten in de verschillende behandelingen constant gehouden.

Invloed minder geconcentreerde voeders op welzijn vleeskuikenouderdieren

Bij het verstrekken van minder geconcentreerde voeders aan vleeskuiken-ouderdieren zijn zowel tijdens de opfok- als tijdens de legperiode verschillende kenmerken gemeten die gerelateerd zijn aan hongergevoel, de mate van chronische stress en de voeropnamemotivatie van de dieren. Hierbij werd het gedrag van de ouderdieren op verschillende leeftijden bestudeerd. Daarnaast werden de dieren onderworpen aan een voeropnamemotivatietest. Op basis van eerder uitgevoerd onderzoek is gebleken dat veel stereotiep pikgedrag en een hoge mate van activiteit wijzen op meer honger en chronische stress. Een hoge voeropname in de voeropnamemotivatietest wijst op een grotere motivatie om voer op te nemen en duidt op een sterker hongergevoel. In het bloed van de dieren werd het corticosterongehalte en de verhouding tussen heterofielen en lymfocyten vastgesteld. Hogere waarden hiervan wijzen op het optreden van stress. Verder werden in het bloed de gehalten aan glucose en vrije vetzuren (NEFA) gemeten. De resultaten van deze bepalingen zijn in hoofdstuk 3 beschreven.

Minder geconcentreerde voeders gaven een toename van de voeropnametijd. Deze toename was het grootst tijdens de legperiode (tot 373 %). LD23 voeders gaven een significante afname van stereotiep pikgedrag en een significante toename van de tijd dat de dieren rusten op een leeftijd van 6 en 10 weken. In week 16 en 20 werden geen verschillen in gedrag tussen de behandelingen waargenomen. LD23 en LD12^{OP} voeders gaven een afname van de compensatoire voeropname in de voeropnamemotivatietest op een leeftijd van 12 weken. De afname in compensatoire voeropname was bij LD12^{OP} voer significant groter dan bij LD12 voer. Dit betekent dat grondstoffen en het vezeltype invloed kunnen hebben op de mate van verzadiging van ouderdieren. Tijdens de opfokperiode werden tussen de dieren in de verschillende behandelingen geen verschillen in heterofiel/lymfocyt-ratio en corticosterongehalten in het bloed waargenomen. De glucose/NEFA-verhouding nam significant toe in week 10 en 26 in LD23. De veranderingen in gedrag en de verschillen in compensatoire voeropname in de voeropnamemotievatietest, duiden op een minder groot hongergevoel gedurende de eerste helft van de opfok. De resultaten van de voeropnamemotivatietest duiden op een toename van de fysieke verzadiging in LD23 en LD12^{OP}. Hierbij moet worden opgemerkt dat het voer in de voeropnamemotivatietest onbeperkt werd verstrekt.
Tijdens de legperiode besteedden de dieren die minder geconcentreerde voeders ontvingen meer tijd aan het opnemen van voer en minder tijd aan zitten. Op een leeftijd van 40 weken gaf LD21 een significante toename van de heterofiel/lymfocyt-ratio in het bloed. Dit duidt op een toename van stress in LD21 dieren in vergelijking met dieren op andere voeders. LD21 geeft dus geen verbetering van het welzijn tijdens de legperiode.

Invloed minder geconcentreerde voeders op ontwikkeling vleeskuikenouderdieren en nutriëntenverteerbaarheid

In hoofdstuk 4 is de ontwikkeling van de ouderdieren tijdens de opfokperiode beschreven en is de verteerbaarheid van de verschillende voeders gegeven. Bij de ontwikkeling van de ouderdieren is vooral de ontwikkeling van de reproductie organen bestudeerd. De reden hiervoor was dat in eerder uitgevoerd onderzoek was gebleken dat het eigewicht bij het verstrekken van minder geconcentreerde voeders niet toenam als deze voeders alleen tijdens de legperiode werden verstrekt. Het verstrekken van minder geconcentreerde voeders tijdens zowel de opfok- als de legperiode resulteerde in eerder uitgevoerd onderzoek wel in een significante toename van het eigewicht.
Uit de resultaten, die in hoofdstuk 4 zijn beschreven, bleek dat het verstrekken van LD12^{OP} voer een significant lager lichaamsgewicht gaf aan het eind van de opfokperiode. Dit lagere lichaamsgewicht werd toegeschreven aan een lagere nutriëntenopname, die werd veroorzaakt doordat de verteerbaarheid van dit voer lager was dan was verwacht. De LD23 en LD12^{OP} voeders gaven een lager ovarium-

en oviductgewicht in week 24 in vergelijking met ND voer. Deze minder goede ontwikkeling van de reproductie organen wordt ook waargenomen bij het sterker beperken van de voergift tijdens de opfokperiode. De minder goede ontwikkeling van de reproductie organen in week 24 werd gecompenseerd in de periode van week 24-26. De verschillen in ontwikkeling van de ouderdieren en reproductie organen werden toegeschreven aan verschillen in nutriëntenverteerbaarheid en de benutting van verteerde nutriënten tussen voeders. Uit het verteringsonderzoek bleek dat minder geconcentreerde voeders geen toename gaven van de inhoud van het maagdarmkanaal. Hiermee lijkt de fysieke verzadiging niet toe te nemen bij het verstrekken van minder geconcentreerde voeders bij een beperkte voergift.

Invloed minder geconcentreerde voeders op reproductie vleeskuikenouderdieren

De effecten van minder geconcentreerde voeders op legprestaties, de eisamenstelling en de embryonale ontwikkeling zijn in hoofdstuk 5 beschreven. De hypothese hierbij was dat veranderingen in de ontwikkeling van de reproductie organen, zoals deze in hoofdstuk 4 zijn beschreven, invloed hebben op de legprestaties en de eisamenstelling. Eventuele effecten van minder geconcentreerde voeders op de prestaties en de vitaliteit van de nakomelingen zouden via het ei moeten worden overgedragen.

$LD11^{OP}$ voeders gaven tijdens de legperiode een significant lager lichaamsgewicht in vergelijking met de andere voeders. De LD11 voeders resulteerden in een significante toename van het legpercentage in vergelijking met de ND voeders. Het eigewicht nam significant toe wanneer minder geconcentreerde voeders werden verstrekt, ook als dit alleen in de opfokperiode gebeurde. De toename van het eigewicht werd toegeschreven aan veranderingen in de ontwikkeling van de reproductie organen aan het eind van de opfokperiode.

De toename van het eigewicht bij het verstrekken van minder geconcentreerde voeders bleek het gevolg te zijn van een toename van de hoeveelheid ei-wit in het ei. De hoeveelheid dooier bleef gelijk. LD21 voeders resulteerden in een significant betere ontwikkeling van de area vitellina externa (eerste aanleg darm) en gaven een hoger hart- en embryogewicht in eieren van 29 weken oude ouderdieren. De betere embryonale ontwikkeling werd toegeschreven aan het toegenomen ei- en witgewicht. Verschillen in schaalkwaliteit, die tijdens het broedproces een hoger vochtverlies in eieren van ouderdieren uit de ND groep ten opzichte van die uit de LD21 groep zouden kunnen verklaren, kunnen ook van invloed zijn geweest op de verschillen in embryonale ontwikkeling.

Invloed minder geconcentreerde voeders op prestaties en vitaliteit nakomelingen

Op basis van de effecten van minder geconcentreerde voeders op het eigewicht, de eisamenstelling en de embryonale ontwikkeling, werd nagegaan in hoeverre deze verschillen invloed hadden op de technische resultaten, de uitval en de humorale afweer van de kuikens. Van de ouderdieren werden hiertoe op een leeftijd van 29, 41 en 60 weken broedeieren verzameld en uitgebroed. Voordat de eieren werden uitgebroed, werden deze verdeeld in een zware en lichte gewichtsklasse om het gewicht van het eigewicht op de prestaties, vitaliteit en humorale afweer te kunnen bepalen. Hierdoor zou kunnen worden aangegeven of eventuele verschillen tussen kuikens uit de verschillende behandelingen het gevolg zijn van verschillen in eigewicht of dat deze kunnen worden toegeschreven aan andere, meer specifieke, effecten van het verstrekken van minder geconcentreerde voeders. De resultaten van de kuikenproeven zijn beschreven in hoofdstuk 6.
Het verstrekken van minder geconcentreerde voeders aan de ouderdieren tijdens zowel de opfok- als de legperiode en tijdens alleen de opfokperiode resulteerde in een significante toename van het gewicht van eendagskuikens. Op een leeftijd van 38 dagen gaf het verstrekken van LD11 voer aan de ouderdieren een significante toename van het kuikengewicht. Deze toename was het duidelijkst in de kuikens die afkomstig waren uit de lichte broedeieren. Verschillen in kuikengewicht werden in verband gebracht met verschillen in eigewicht en met een hogere opname van verteerbare nutriënten door de ouderdieren die LD11 voer kregen.
Minder geconcentreerde ouderdierenvoeders gaven bij kuikens van 60 weken oude ouderdieren een significant lager uitvalspercentage in vergelijking met de ouderdierenvoeders met een normale nutriëntendichtheid. Dit was ook het geval als het minder geconcentreerde voer alleen tijdens de opfokperiode werd verstrekt. In kuikens van 29 en 41 weken oude ouderdieren werden geen verschillen in uitval waargenomen tussen de behandelingen. De uitval was gemiddeld laag in de proeven met deze kuikens. In eerder uitgevoerd onderzoek werd een significant lagere uitval bij de kuikens van 26 en 40 weken oude ouderdieren waargenomen wanneer aan de ouderdieren minder geconcentreerde voeders werden verstrekt.
Voor het vaststellen van de invloed van minder geconcentreerde ouderdierenvoeders op de humorale immuniteit van de nakomelingen werden bij de kuikens IgM- en IgG-titers na herhaalde immunisatie gemeten. IgM-titers in kuikens uit lichte eieren van 29 weken oude ouderdieren waren significant lager wanneer minder geconcentreerde voeders werden verstrekt. In kuikens uit zware eieren van 60 weken oude ouderdieren werden significant hogere IgM-titers waargenomen in LD11 en LD21 ten opzichte van ND. De verschillen in uitval en titers werden gerelateerd aan verschillen in eigewicht en eisamenstelling tussen de voeders. De verschillen in titers tussen behandelingen, eigewichtsklassen en leeftijden van de ouderdieren geven aan dat nutriënten in eieren met een relatief laag gewicht eerder worden gebruikt voor lichaamsgroei dan voor de ontwikkeling van het humorale immuunsysteem.

Conclusies

Op basis van de resultaten, die in dit proefschrift zijn beschreven, kunnen de volgende conclusies worden getrokken:

- Minder geconcentreerde voeders kunnen een afname geven van stereotiep pikgedrag en kunnen resulteren in een toename van de tijd dat dieren zitten tijdens de eerste 10 weken van de opfokperiode. Dit duidt op een verbetering van het welzijn van de ouderdieren. Hierbij dient het nutriëntengehalte van het voer met meer dan 20 % te worden verlaagd. Wanneer minder geconcentreerde voeders onbeperkt aan ouderdieren worden verstrekt, geven deze een lagere compensatoire voeropname. Dit duidt op een toename in verzadiging bij het verstrekken van deze voeders. Dit effect op de voeropnamemotivatie is afhankelijk van de grondstoffen die in het minder geconcentreerde voer worden verwerkt: het effect is groter bij het verwerken van haver en bietenpulp dan bij het verwerken van palmpitschilfers, tarwegries, tarweglutenvoer en zonnebloemzaadschroot. Het verstrekken van minder geconcentreerde voeders geeft geen toename van de inhoud van het maagdarmkanaal. Dit is het gevolg van een toename van de passagesnelheid van de digesta.
- Het verstrekken van minder geconcentreerde voeders geeft tijdens de legperiode een sterke toename van de tijd die aan het opnemen van voer wordt besteed. Het verstrekken van deze voeders kan een toename geven van de heterofiel/lymfocyt-verhouding wanneer het nutriëntengehalte in het voer met meer dan 20 % wordt verlaagd. Dit duidt op een verslechtering van het welzijn van de ouderdieren, waardoor tijdens de legperiode het verstrekken van voeders met een sterk verlaagde nutriënteninhoud niet zinvol is.
- Minder geconcentreerde opfokvoeders kunnen een uitstel geven van de ontwikkeling van het ovarium en het oviduct. Dit kan resulteren in een toename van het eigewicht tijdens de gehele legperiode. De toename van het eigewicht is het gevolg van een toename van de hoeveelheid wit in het ei. Het uitstel in de ontwikkeling van het ovarium en het oviduct kan worden toegeschreven aan een lagere nutriëntenverteerbaarheid en een minder goede benutting van de verteerde nutriënten wanneer minder geconcentreerde voeders worden verstrekt.
- Wanneer minder geconcentreerde voeders beter worden verteerd dan vooraf was verwacht en hierdoor resulteren in een hogere opname van verteerbare nutriënten, kunnen deze een toename geven van het legpercentage. Dit is het geval wanneer het nutriëntengehalte van het voer met ongeveer 12 % wordt verlaagd.
- Het verstrekken van minder geconcentreerde voeders aan ouderdieren geeft een verbetering van de vroege ontwikkeling van de area vitellina externa (eerste aanleg darm) en geeft een toename van het embryogewicht. Deze toename in ontwikkeling kan worden toegeschreven aan een toename van het eigewicht en de toename van de hoeveelheid wit in het ei.

- Het verlagen van het nutriëntengehalte in het ouderdierenvoer met ongeveer 12 % kan een toename geven van de groei van de kuikens afkomstig van jonge ouderdieren door een hogere opname van verteerbare nutriënten door de ouderdieren.
- Het verstrekken van minder geconcentreerde voeders aan vleeskuiken-ouderdieren kan een afname geven van het uitvalspercentage van de nakomelingen. Dit is ook het geval als minder geconcentreerde voeders alleen tijden de opfokperiode worden verstrekt. Hierbij kan worden volstaan met het verlagen van de nutriëntendichtheid van het voer met ongeveer 12 %. De afname van het uitvalspercentage kan worden gerelateerd aan een toename van het eigewicht en de hoeveelheid wit in het ei wanneer minder geconcentreerde voeders aan de ouderdieren worden verstrekt. In het onderzoek werden geen aanwijzingen gevonden voor veranderingen in stressniveaus bij de ouderdieren bij het verstrekken van minder geconcentreerde voeders. Hiermee lijkt er geen verband te zijn tussen stressniveaus bij de ouderdieren en het uitvalspercentage van de nakomelingen.
- Minder geconcentreerde ouderdierenvoeders geven een afname van de IgM- en IgG-titers in nakomelingen uit eieren met een relatief laag gewicht van ouderdieren van 29 weken oud. In nakomelingen uit eieren met een relatief hoog gewicht van 60 weken oude ouderdieren geven deze voeders een toename van de IgM- en IgG-titers. De resultaten geven aan dat nutriënten in eieren met een relatief laag gewicht eerder worden gebruikt voor lichaamsgroei dan voor de ontwikkeling van het humorale immuunsysteem.

Training and Supervision Plan			Graduate School WIAS
Name PhD student	Henk Enting		
Project title	Effect of low-density diets on broiler breeder and offspring performance		
Group	Animal Nutrition		
Daily supervisor(s)	Dr. Ir. P.J. van der Aar		
Supervisor(s)	Prof. Dr. Ir. M.W.A. Verstegen		
Project term	from: 2001	until: 2005	
Submitted	date: 17-5-2005	first plan / midterm / **certificate**	

EDUCATION AND TRAINING (minimum 21 cp, maximum 42 cp)		
The Basic Package (minimum 2 cp)	year	cp*
WIAS Introduction Course (mandatory)	2003	1,0
Course on philosophy of science and/or ethics (mandatory)	2003	1,0
Subtotal Basic Package		**2,0**
Scientific Exposure *(conferences, seminars and presentations, minimum 5 cp)*	*year*	*cp*
International conferences *(minimum 2 cp)*		
European Poultry Science Symposium, Bremen, Germany, September 2002	2002	0,8
World Poultry Conference, Istanbul, Turkey, June 2004	2004	0,8
Australian Poultry Science Symposium, Sydney, Australia, February 2005	2005	0,8
Seminars and workshops		
Intercoop Poultry Nutrition Workshops	2001-2004	0,8
Presentations *(minimum 4 original presentations of which at least 1 oral, 0.5 cp each)*		
European Poultry Nutrition Symposium, Blankenberge, Belgium, September 2001 (oral)	2001	0,5
Intercoop Feedstuffs Congress, Oslo, Norway, June 2003 (oral)	2003	0,5
European Poultry Nutrition Symposium, Lillehammer, Norway, August 2003 (oral)	2003	0,5
World Poultry Conference, Istanbul, Turkey, June 2004 (oral)	2004	0,5
Western Nutrition Conference, Saskatoon, Canada, September 2004 (oral)	2004	0,5
Australian Poultry Science Symposium, Sydney, Australia, February 2005 (oral)	2005	0,5
International Symposium on Nutritional Requirements, Vicosa, Brazil, March 2005 (oral)	2005	0,5
Subtotal International Exposure		**6,7**
In-Depth Studies (minimum 4 cp)	year	cp
Disciplinary and interdisciplinary courses		
POA course metabolic disorders in poultry	2002	1,0
POA course rearing and laying disorders	2004	0,4
POA course problems during laying	2004	0,4
PhD students discussion groups *(optional)*		
Monthly discussions about animal nutrition research projects at Schothorst Feed Research	2001-2003	2,5
Subtotal In-Depth Studies		**4,3**
Professional Skills Support Courses (minimum 2 cp)	year	cp
Use of Laboratory Animals (mandatory when working with animals)	1992	3,0
Subtotal Professional Skills Support Courses		**3,0**
Research Skills Training (optional)	year	cp
Preparation of own PhD research proposal	2002	4,0
Subtotal Research Skill Training		**4,0**
Didactic Skills Training (optional)	year	cp
Lecturing		
Farmer study groups and presentations for animal feed companies	2001-2005	4,0
Preparation of course material		
Poultry nutrition courses for the animal feed industry	2001-2005	4,0
Subtotal Didactic Skills Training		**8,0**
Management Skills Training (optional)	year	cp
Organisation of seminars and courses		
Intercoop Poultry Nutrition Workshops	2001-2004	4,0
Membership of boards and committees		
CVB working group Physiological Nutrition Strategies	2001-2004	2,0
Subtotal Management Skills Training		**6,0**
Education and Training Total (minimum 21 cp, maximum 42 cp)		**34,0**

Curriculum vitae

Henk Enting werd op 15 oktober 1966 geboren te Zuidveld, gemeente Westerbork. Na het doorlopen van de lagere school behaalde hij in 1985 het VWO-diploma op de Christelijke Scholengemeenschap De Baander te Emmen. In datzelfde jaar werd met de studie Zoötechniek aan de Landbouwuniversiteit te Wageningen begonnen. Deze studie werd in augustus 1991 met lof afgerond met als afstudeervakken Veefokkerij, Veevoeding en Agrarische Bedrijfseconomie. Van augustus 1991 tot mei 2005 was hij werkzaam als onderzoeker Pluimveevoeding op het Instituut voor de Veevoeding 'De Schothorst' te Lelystad. Sinds 1 mei 2005 werkt hij als onderzoeker op het Poultry and Rabbit Research Centre van Nutreco in Spanje.

Drukker

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