UNIVERSITY OF ALBERTA

IMPLICATIONS OF NUTRIENT DILUTION ON THE WELL-BEING AND PRODUCTIVITY OF FEMALE BROILER BREEDERS

BY

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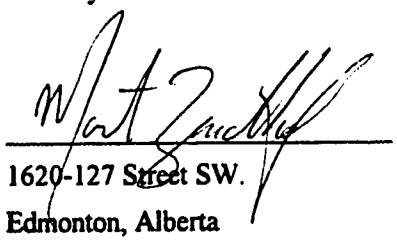

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It's what you learn after you know it all that really counts.
Harry. S. Truman

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled IMPLICATIONS OF NUTRIENT DILUTION ON THE WELL-BEING AND PRODUCTIVITY OF FEMALE BROILER BREEDERS submitted by MARTIN JACOB ZUIDHOF in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE IN ANIMAL PRODUCTION.

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Abstract

Four hundred and eighty broiler breeder pullets were reared in six floor pens. Commercial age-appropriate diets were provided undiluted and diluted 15% and 30% with ground oat hulls. Daily feed allocations were provided to achieve the breeder's recommended body weights. At 20 weeks the pullets were photostimulated, and at 22 weeks 240 pullets (80 per treatment) were moved to 120 laying cages. They remained in these cages until 56 weeks of age and received the same dilution treatments as during the rearing period. The remaining pullets were kept in floor pens until 49 weeks of age.

The time required to consume all allocated feed was longer for birds fed the diluted diets during both the rearing period ($P=0.002$) and the laying period ($P=0.0001$). Flock uniformity did not differ significantly ($P<0.05$) among treatments during the rearing or laying periods, however from the time of photostimulation to the end of the study, flock uniformity decreased at a greater rate in cages receiving the undiluted diet than in cages where diluted diets were fed ($P<0.05$). The heterophil / lymphocyte (H/L) ratio at 12 weeks of age was reduced in the birds fed diluted diets ($P=0.0004$), indicating reduced stress. At 20 weeks of age the H/L ratio did not differ, indicating that the pullets fed the undiluted ration may have been able to adapt to the stress. At 54 weeks of age the H/L ratio was also not significantly different, probably because the level of restriction during lay was much less severe than that implemented during rearing. During the laying period the hens receiving the undiluted diet were observed to spend more time at the drinker than hens which were fed diluted diets ($P=0.0001$). Analysis of stereotypical spot-pecking behavior was inconclusive. Hens in the 15% dilution treatment had the highest rate of egg production ($P=0.0121$), the highest incidence of days with multiple ovulations (double yolked egg or two eggs in one day ($P=0.02$)), and the greatest feed conversion efficiency as a function of total feed intake as well as CP intake ($P<0.05$). Diet dilution with ground oat hulls is recommended at a level of 15% for reducing hunger stress and improving productivity and efficiency compared to undiluted diets or more dilute (30%) diets.

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Chapter 1 - Implications of *ad libitum* feeding *versus* feed restriction in broiler parent stock

Introduction

During the past 50 years, there have been many remarkable improvements in the efficiency of poultry production. In meat-type chickens, selection for feed efficiency, growth rate, body composition (ratio of fat to lean), and meat yield have resulted in a dramatically improved growth performance and product quality. For example, the feed conversion of broilers has improved from 4.70 kg feed per kg gain in body weight in 1940 to 1.90 kg feed per kg gain in body weight in 1990 (Robinson, 1991). Due to a combination of genetic selection and improved nutrition, the same quantity of chicken can be produced today in less time and with less than half of the feed that was required 50 years ago.

The rapid growth rate and large body size of modern meat type chickens, however, have serious drawbacks for parent stock. There is a negative relationship between body weight (BW) and reproductive performance in broiler breeders (Robinson *et al.* 1993a) and turkey breeders (Miles and Leeson 1990). When broiler breeder hens are allowed to eat *ad libitum*, they become obese, and lose physiological control of ovarian function. As a result, egg production is significantly reduced (Robinson *et al.* 1991, Yu *et al.* 1992c, Robinson *et al.* 1993a). Reproductive anomalies common in obese hens include an increased incidence of erratic laying (eggs laid outside of the normal range of time, from dawn to approximately 8 hours after first light), as well as reduced shell quality, fertility, hatchability, and chick quality. However, the mechanism responsible for the decreased productivity is unclear. In spite of an increase in ovarian follicle numbers with *ad libitum* feeding, reproductive output in full fed hens is decreased (Robinson *et al.* 1991, Yu *et al.* 1992c). Although fat is negatively associated with egg production (Bornstein *et al.* 1984, Robinson *et al.* 1991, Yu *et al.* 1992b), fat *per se* does not appear to cause decreases in fertility (Bilgili and Renden 1984). The negative relationship between obesity and productivity has forced

the broiler breeder industry to adopt feed restriction as a standard practice for controlling BW gain and thus maximizing the productivity of female breeders.

Although feed restriction may delay the onset of sexual maturity of broiler breeder pullets (Yu *et al.* 1992b), there is an improvement in overall egg production (Robinson *et al.* 1991, Fattori *et al.* 1991, Yu *et al.* 1992c), persistency of lay (Fattori *et al.* 1991), and ovarian control. Feed restriction has resulted in longer sequence lengths (*i.e.* consecutive days on which eggs are laid), fewer and shorter intersequence pauses (Robinson *et al.* 1991), decreased erratic laying (Yu *et al.* 1992c), fewer defective eggs, and fewer multiple ovulations (Yu *et al.* 1992c, Fattori *et al.* 1991). Fattori *et al.* (1991) reported that egg production at 64 weeks was significantly higher in birds kept 16% and 24% below the breeder's recommended BW. Even more severe levels of restriction than those currently recommended by primary breeders may result in improved overall egg production by improving the persistency of lay (Robinson, unpublished data). With more severe feed restriction a longer production period than currently utilized may become economically feasible.

The ovulatory cycle

Overview

Egg production in birds is the result of the finely tuned regulation of the ovulatory system. In order to understand reproductive problems in the domestic hen, it is important to understand the anatomy and the normal function of the avian reproductive system. Chickens, like all members of the class Aves are oviparous, that is, they posit eggs in which embryonic development occurs. The eggs subsequently hatch to release viable young. The development of the egg occurs along the entire reproductive tract of the female. The following sections describe normal reproductive function and explore the mechanisms of reproductive malfunction in the domestic hen.

The ovary and ovum

In birds, only the left ovary and oviduct normally develop (Burke 1984). The left ovary is attached to the dorsal wall of the abdomen, just anterior to the left kidney. In ontogeny, the kidney and the ovary of the female (and testis of the male) are derived from the same parent tissue. The ovary is a relatively large organ in adult hens. It comprises approximately 2.0 to 2.5% of the body weight of a reproductively active hen (Burke 1984). Over 90% of this weight is in the form of follicles. The ovary consists of a stalk, a cortex, and a medulla. The medulla is rich in nervous, vascular, and connective tissue (Gilbert 1969, Burke 1984). The cortex of a normal active Single Comb White Leghorn (egg type hen) ovary contains several thousand small white follicles (SWF) which are less than 1 mm in diameter; approximately ten large white follicles (LWF) which measure 1-5 mm in diameter, about five small yellow follicles (SYF), 5-10 mm in diameter, and a hierarchy of five to seven large yellow follicles (LYF) which are greater than 10 mm in diameter (Robinson and Etches 1986). The LYF are categorized (F1-F7) on the basis of size and proximity to ovulation, with F1 being the largest LYF, and closest to ovulation (Robinson and Etches 1986). These LYF, which have the appearance of egg yolks, give the avian ovary its characteristic appearance.

The immature follicle consists of an oocyte surrounded by follicular cells. As a follicle matures, yolk is deposited around these cells, and the yolk is in turn surrounded by the perivitelline membrane (Burke 1984). Granulosa cells surround the perivitelline membrane, and are in contact with the yolk by means of processes which penetrate the perivitelline membrane (Burke 1984). A thecal layer surrounds the granulosa layer. The granulosa and theca interna layers are the primary regions of steroidogenesis (Etches 1990). The follicle is nurtured by a network of veins and arteries. The stigma of the follicle is distinguishable by its lack of vascularization, and is the site of rupture at the time of ovulation (Burke 1984, Grau 1984).

Control of reproduction

The reproductive cycle of the domestic fowl varies from approximately 22 to 28 hours in length (Etches 1990). A direct result of this phenomenon is that birds lay eggs in clutches or sequences (consecutive days on which eggs are laid). Determinate layers such as ducks and geese lay a single clutch of four to ten or more eggs, after which the ovary regresses back to a dormant state (Smith 1986). Indeterminate layers, on the other hand, may continue to lay successive sequences. These sequences may contain any number of eggs (from one to in excess of 100), and are separated by a pause of one or more days in length. When exposed to ahemeral (≠24 hr) photoschedules such as 16L:7D (23 hr days), hens with the ability to produce a mature follicle in 23 hours may still be capable of laying one egg every 23 hr day.

The onset of reproduction is normally stimulated by increasing day-length. The response to light does not appear to occur at the level of the eye or the pineal gland (reviewed by Kuenzel 1993); it is more likely that light stimulates deep encephalic photoreceptors in the ventral forebrain, possibly the medial basal hypothalamus (Kuenzel 1993). There is also evidence that in migratory birds the timing of ovarian development is closely linked to the arrival at the nesting grounds (somewhat independent of exact daylength), and may therefore also be stimulated by nesting behavior (Raveling 1978). Photostimulation initiates two signals to Gonadotropin Releasing Hormone-I (GnRH-I) neurons in the hypothalamus (Sharp 1993). One input is positive, causing a release of GnRH and the other, negative, is slower to develop. GnRH causes a release of Gonadotropins (Luteinizing Hormone (LH) and Follicle Stimulating Hormone (FSH)) from the anterior pituitary of the bird. LH initiates the production of dehydroepiandrosterone (DHEA), androstenedione and estradiol in the SWF (Robinson and Etches 1986). LH also stimulates the production of progesterone in the granulosa cells of the SWF (reviewed by Robinson and Etches 1986), the conversion of progesterone to testosterone in the thecal cells, and the production of estrogens in thecal and granulosa cells (Grau 1984). Follicle recruitment may be the result of either hormonal or direct nervous stimulation of small follicles, although the exact mechanism of follicular

recruitment remains unknown (Grau 1984). The events stimulated by the increase of photoperiod, however, result in the recruitment of follicles into a period of rapid growth when yolk is deposited at an accelerated rate. The result of the successive recruitment of follicles into the rapid growth phase is the formation of the preovulatory follicular hierarchy.

Follicle maturation and the "open period" for LH release

The ovulatory process is controlled hormonally, and the circadian "clock" which controls the timing of events is reset daily by dusk and daybreak. The "open period" for LH release is a daily window of time in which an LH surge can occur, thus governing the time when ovulation can occur. This window is approximately limited to the period from dusk to about 1 hour after dawn (Sharp 1989), and, unlike follicular maturation, is dependent on photoschedule (Etches *et al.* 1984). Erratic laying may be the result of lost control of the timing of the open period.

It is clear that photostimulation results in increased steroidogenesis. In response to increased plasma estrogen levels, the liver produces lipoproteins in large quantities (Grau 1984). Following follicular recruitment, yolk is manufactured from these lipoprotein precursors, and deposited around the outside of the follicles rapidly for a period of 7 to 11 days in the chicken (Grau 1976). When follicles mature, the theca cells lose their ability to metabolize progesterone to androstenedione (Robinson and Etches 1986). A mature follicle is an F1 follicle which has acquired the ability to ovulate in response to the preovulatory surge of LH. Progesterone levels increase in the mature follicle because of the increased progesterone production in the F3-F1 follicles, and the lost ability to metabolize progesterone to androstenedione (Robinson & Etches 1986, Yu *et al.* 1992a). When a mature follicle is present, positive feedback by progesterone and GnRH continues until the mature follicle(s) respond(s) to the LH surge by ovulating (Shimada and Saito 1989, Etches 1990). Ovulation is the process of follicular rupture followed by the release of the ovum.

In obese hens, simultaneous development of follicles occurs (Hocking *et al.* 1987, 1989, Yu *et al.* 1992c, Robinson 1993b). This means that more than one follicle is recruited in a single day, and these follicles grow simultaneously in the form of multiple hierarchies. A consequence of simultaneous development is that more than one follicle must be cleared from the ovary in a single ovulatory cycle. There are two methods of follicular clearance. The first is atresia, where the follicle regresses as the follicular components are reabsorbed by the hen. A regressing follicle is called an atretic follicle. The second method of follicular clearance is by ovulation of excess follicles, either simultaneously or sequentially. Simultaneous ovulation of excess follicles results in multiple yolked eggs, while sequential ovulation results in eggs with poor shell quality, presumably because the shell gland cannot properly calcify more than one shell per day.

Oviductal function and malfunction

Normally when a follicle matures, it ovulates in response to the pre-ovulatory LH surge. The oviduct is the duct through which the ovum passes by means of peristaltic action from the ovary to the cloaca. Its function is to provide the ovum with the necessary provisions for the 21 day development period outside of the hen's body. The oviduct can be subdivided into five main components. From the ovary, they are the infundibulum, the magnum, the isthmus, the shell gland, and the vagina. The infundibulum is a very thin, lightly muscularized tissue, which acts as a gently undulating funnel which engulfs the ovum as it is ovulated (Grau 1984) and directs it into the oviduct. The infundibulum is considered to be the site of fertilization (Burke 1984). The magnum, which follows the infundibulum, is the longest portion of the oviduct. It is lined with albumen secreting glands. Albumen accretion around the ovum occurs in the magnum. After 2 to 3 hours of albumen deposition in the magnum, the egg passes through the isthmus. The isthmus, distal to the magnum, is the region of the oviduct which secretes a fibrous substance which forms two thin membranes around the albumen. These membranes are very important in the determination of egg shape. Approximately 4 to 5 hours after ovulation the egg reaches the shell gland. In the shell gland, calcium carbonate is deposited around the egg membranes in a protein

matrix to form a hard shell. The process of shell formation normally continues for approximately 20 hours. Once calcification is completed, the egg passes through the vagina which opens into the cloaca, and the egg is expelled in a process termed oviposition.

Ovulation of a subsequent follicle stimulates oviposition (Shimada and Saito 1989). Prostaglandins (PGs) are released from the mature follicle and the largest post-ovulatory upon ovulation. The release of PG stimulates contractions in the smooth muscle of the shell gland. This results in the expulsion of the egg from the shell gland (Shimada and Saito 1989). Etches (1990) indicated that the time that the terminal egg of a sequence is laid is later than expected based on the pattern established by earlier eggs in a sequence. The reason for this may be that the PGs released from the mature follicle upon ovulation stimulate the release of PGs from the largest post-ovulatory follicle. In the case of the terminal egg of a sequence, ovulation does not precede oviposition. Therefore there is no PG signal to initiate oviposition. In this case, the release of PGs from the largest post-ovulatory follicle may occur spontaneously approximately 27 hours after ovulation, as oviposition of the last egg occurs without the ovulatory signal.

The incidence of abnormal eggs in broiler breeders increases with *ad libitum* feeding (Yu *et al.* 1992c). It is possible to trace some of the defects to malfunctions of the ovary, and subsequent or independent problems in the oviduct. The frequency of malfunction increases with the degree of hen obesity (Robinson, unpublished observation) and age (Bahr and Palmer 1989).

It is probable that the hen cannot effectively accommodate two eggs in the oviduct simultaneously, although two eggs in the oviduct is not uncommon in parent stocks of meat type breeders (Robinson, unpublished observation). In obese hens, the frequency of erratic ovipositions increases (Yu *et al.* 1992c, Robinson *et al.* 1993a). This may indicate either that excess follicles are cleared sequentially, or the normal timing of the open period may be displaced. Erratic laying

correlates positively with poor shell quality and negatively with settable egg production (Yu *et al.* 1992c). The net result of erratic laying is undesirable from the production perspective, since it translates into fewer hatchable eggs.

If ovulation of two or more follicles occurs sequentially and they are transported simultaneously through the oviduct, the result is a multiple yolked egg. In the case of multiple yolked eggs, the albumen, membranes and shell are all deposited around two or more yolky follicles. These eggs are unusable as hatching eggs since they do not produce viable embryos (Robinson, unpublished data). Alternately, if passage through the oviduct is not simultaneous, due either to the delay of one simultaneously ovulated ovum or sequential ovulation, egg formation may occur independently. When the subsequent ovum completes the journey through the oviduct, the first egg is laid before a quality shell is formed. The result is a single yolked egg with a poor shell or no shell. Alternately, if the presence of a second egg in the shell gland does not induce oviposition, a shell may form around the new egg and the initial egg, resulting in a partially or fully shelled egg within an egg.

Oviductal abnormalities that may occur independently of ovarian malfunctions include internal ovulation and internal laying. In the case of internal ovulation, the infundibulum fails to engulf the ovulated follicle, and the follicle is released into the body cavity. Evidence of this phenomenon is yolky follicles in the body cavity which have been found upon dissection. A second, more puzzling oviductal malfunction is internal laying. In the case of internal laying, an egg completes its journey through the oviduct normally. Then for some unknown reason the egg is transported back up the oviduct, most likely by the process of reverse peristalsis. This phenomenon is evidenced by the presence of fully formed eggs (albumen and membranes) with various levels of shell calcification in the body cavity upon dissection. There is evidence for multiple malfunctions of

this sort in individual birds, the frequency of which increases with hen weight (Robinson, unpublished observation).

Much of the normal functioning of the ovulatory cycle is well understood. However, many questions remain. For example, the mechanisms controlling follicular recruitment remain unclear. A better understanding of the control of this process may help animal scientists to discover how to reduce the number of multiple hierarchies in large hens by controlling excess follicular recruitment. Subsequent oviductal problems could be reduced in this way. Much descriptive work remains, and the underlying physiological control mechanisms need to be deciphered in order to discover how the normal reproductive system is affected by environmental factors such as excessive feed, or how a "stressor" such as feed restriction improves reproductive efficiency in meat-type breeder hens.

Flock uniformity concerns in broiler breeders

Although feed restriction is necessary from a production standpoint, it also presents problems which must be addressed. Two concerns arising from feed restriction are flock uniformity and metabolic stasis. Broiler breeder flocks with the same mean body weight may have different degrees of uniformity. A flock managed by mean BW may still manifest problems associated with obese birds and light birds because of disuniformity in BW. It stands to reason, therefore, that good flock management should include some means of maximizing flock uniformity.

Various feed restriction protocols have been proposed which involve the provision of feed daily, every second day, or even every third day. "Skip day" protocols are commonly used to facilitate management and to improve flock uniformity and efficient nutrient utilization (Bartov *et al.* 1988), however availability of feed more often may be important for the efficient maintenance of homeostasis and for bird well-being. Daily feed restriction (DFR) is a preferable feed restriction method from both a metabolic and an animal welfare perspective. DFR protocols involve providing a pre-calculated allotment of feed daily, in order that the birds do not exceed

recommended BW for maximum productivity. Since competition for a limited amount of feed from limited feeder space may result in increased agonistic behavior (Bennet and Leeson 1989) and disproportionate feed distribution among birds within the flock (Petitte *et al.* 1982, Bennet and Leeson 1989, Karunajeewa 1987) provision of adequate feeder space is imperative. It has been demonstrated that with "skip a day" (S1D) feeding, ample feeder space does not necessarily mean that all birds must eat simultaneously (van Krey and Weaver 1988). More feed is given at one time in S1D than DFR regimes; the pullets may reach satiety and leave the feeding area, thus allowing less aggressive pen mates to eat. Conversely, pullets subjected to DFR do not likely reach the point of satiety. Ample feeder space for DFR regimes may therefore involve the provision of enough space for all birds to eat simultaneously.

S1D and "skip two days" (S2D) protocols have been investigated in order to decrease the flock uniformity problems associated with DFR regimens (Bartov *et al.* 1988). The more severe feed restriction method (S2D) did result in improved flock uniformity. Quantitative feed restriction causes variability in the circulating levels of nutrients, and presumably is costly because of the energy required for nutrient storage during times of excess nutrient availability, and retrieval when the nutrients are required. Bartov *et al.* (1988) documented greater variation in levels of blood glucose in the more severe restriction regime. Reproductive output was not affected by the feed restriction protocol.

An alternate means of improving flock uniformity is by segregating birds according to body weight and feeding diets with different nutrient concentrations (Petitte *et al.* 1981). In this management regime, repeated segregation would probably be more effective than a single segregation at 4 weeks of age, since the birds within separate groups also tend to deviate in BW due to social dominance factors involved at the time of feeding (Petitte *et al.* 1981). Currently, this is not a

practical solution on a commercial level. An automated system for weighing and sorting birds would be necessary, and the cost-effectiveness would need to be assessed.

Compared to quantitative feed restriction, qualitative feed restriction would decrease the competitive advantage of large birds over small birds at the feeder. When access to a limited amount of high quality feed is restricted a shortage of feeder space would contribute to a greater variation in BW because birds do not reach the point of satiety. Gaining access to feed is presumably quite difficult for small or less aggressive birds. If ample diet dilution were implemented, the larger more aggressive birds would reach satiety and vacate the area of the feeder before the feed disappeared completely, thus making feed available to the smaller less aggressive birds, and perhaps to birds which simply eat slowly. The result would be a more uniform distribution of feed and therefore more uniformity in BW within the flock. Egg production may improve for two reasons. First, the number of large hens which are above the optimal BW for egg production would be reduced, and second, the number of small hens which receive more feed than required for maintenance and egg production would also be reduced.

Metabolic considerations for nutrient restriction

One of the primary benefits of nutrient dilution over quantitative feed restriction is the relative metabolic stability which results from the decrease in temporal variation in nutrient availability. With a low nutrient density and high volume feed, the gut contains a relatively consistent supply of nutrients which are available to meet metabolic requirements for a greater portion of the day. The diet may be so dilute, however, that the hen may experience a nutrient deficit at metabolically expensive times of the day, and have to rely on nutrient reserves.

Hatchability is affected by yolk lipid quality (Noble 1987), albumen quality, and shell quality. The protein and energy intakes of the breeder hens play an important role in the resulting fertility and hatchability of eggs (Leeson and Summers 1991). The time that feed is available is also

important for broiler breeder performance. Harms (1991) reported that supplying nutrients late in the day as opposed to the traditional morning feeding resulted in increased shell quality, but egg production decreased, and the hens lost BW. Shell quality would have improved for two reasons. First, calcium is deposited in the egg shell during the late afternoon and night (Farmer *et al.* 1983, Lennards and Roland 1981), and supplying nutrients (including calcium) in the evening increases calcium availability at appropriate times of the day. Secondly, calcium demand decreases with decreased egg production. Therefore shell quality on the smaller number of eggs was improved. Egg production probably decreased because of nutrient deficiencies at metabolically costly times of the day. The open period for the release of LH occurs essentially only during the night. This means that ovulation and the production of large quantities of protein for albumen deposition during the early part of the day must be drawn from reserves stored somewhere in the body. The process of nutrient storage and retrieval is metabolically costly, and decreased egg production may result from inappropriate timing of nutrient availability. The time at which feed is supplied is therefore very important.

Well-being

Introduction

The well-being of farm animals has long been assumed. Most animal owners have a vested (monetary and/or sentimental) interest in their animals, and as a result their care reflects due regard for the animals. However, animal agriculture has been responsible for animal suffering, not necessarily because of cruelty, but as a result of "normal" practices (Rollin 1990). Humans have a moral responsibility to minimize the suffering of the animals we exploit. Webster (1993) pointed out the obligation of livestock producers to their animals:

> "Once we accept that farm animals are not mere live stock [SIC] but sentient creatures with the capacity to suffer we have no option but to assume moral responsibility for their welfare. This does not mean "setting them free" (they have nowhere to go) nor rearing

them "in natural conditions" (traveling in automobiles is not "natural" but we don't complain). Simply expressed, our moral responsibility must be to provide our farm animals with a reasonable quality of life and a gentle death."

Arguments of this type serve to promote reasonable discussion of our responsibility as human beings to provide adequate quality of care for the animals which we exploit.

The "five freedoms" initially set out in the Brambell report (Cmnd. 2836, 1965) have served as a guideline for acceptable standards for farm animal well-being. They have recently been revised to include specific obligations for animal management (Webster 1993). The five freedoms are:

1. *Freedom from thirst, hunger, and malnutrition* - by ready access to fresh water and a diet to maintain full health and vigor.
2. *Freedom from discomfort* - by providing a suitable environment including shelter and a comfortable resting area.
3. *Freedom from pain, injury and disease* - by prevention or rapid diagnosis and treatment.
4. *Freedom to express most normal behavior* - by providing sufficient space, proper facilities and company of the animal's own kind.
5. *Freedom from fear and distress* - by ensuring conditions which avoid mental suffering.

The five freedoms are an approach for understanding animal welfare as perceived by the animal itself. Absolute achievement of the five freedoms (for animals or humans) is unattainable (Webster 1993), and they must therefore not serve as the basis for minimum welfare expectations, and certainly not for legislation.

Stress - the general adaptation syndrome

For many years animals have been known to have similar physiological changes that occur in response to stress, and it has been hypothesized that these physiological changes play a role in the adaptation of species to "nocuous agents" [SIC] or stressors (Selye 1936). Stressors are most

generally defined as any external phenomenon that threatens the life or well-being of an organism. According to the pioneer of stress research, Dr. Hans Selye (1936, 1946), certain biochemical responses appear consistently, independent of the nature of the stressor. The concept of the general adaptation syndrome has originated from these observations.

The general adaptation syndrome generally refers to "all non-specific, systemic reactions of the body which ensue upon long continued exposure to stress" (Selye 1946). The physiological and metabolic changes associated with the general adaptation syndrome have been extensively studied and reviewed (Selye 1946). The general adaptation syndrome occurs in three stages (Selye 1936, 1937, 1946). The "alarm reaction" or "call to arms" is the body's initial response to exposure to stress to which an organism is not adapted. The alarm reaction, which is controlled by the sympathetic nervous system (Harvey *et al.* 1984), occurs in two phases: the "shock phase" and the "counter shock phase". Shock phase symptoms include a short term rise followed by a drop in plasma sugar levels, hypothermia, involution of the lymphatic organs, edema, loss of muscular tone, ulceration of the gastrointestinal tract, the release of adrenaline from the adrenal medullary tissue, and leukopenia (a drop in number of circulating leukocytes) followed by leukocytosis (increase in number of circulating white blood cells) (Selye 1936, 1937, 1946). The counter shock phase involves the reversal of the symptoms of the shock phase, as well as an increase in the production of corticosteroids in the adrenal cortex in order to increase resistance to the stressor (Selye 1946). If the stressor continues to act on the organism, the counter shock phase merges with the second stage of the general adaptation syndrome known as the "stage of resistance", and specific resistance to the stressor reaches its peak. If the stressor is severe enough, habituation is not possible, and the third and final stage, the "stage of exhaustion" manifests itself. Since continued adaptation is no longer possible the animal deteriorates with symptoms similar to those seen in the alarm reaction, and dies (Selye 1937).

Selye's model has been challenged on the basis of its simplicity (Freeman 1985, Rushen 1986). The three stages of the general adaptation syndrome do not invariably follow "noxious stimuli", and the theory is therefore too simple to explain comprehensively the complex biological stress response and adaptive processes.

Indicators of increased adrenal function

Hans Selye (1936) proposed that the hormones produced by the adrenal cortex were responsible for an animal's ability to adapt to "noxious stimuli". There is considerable evidence implicating the Hypothalamo-Pituitary-Adrenal (HPA) axis in the manifestation of stress (reviewed by Harvey *et al.* 1984). Stimuli from the environment are processed and integrated by the CNS. If the stimulus is interpreted as stressful, the HPA axis is activated. Corticotrophin releasing factor (CRF) is released from the hypothalamus, and stimulates the production and release of adrenocorticotrophic hormone (ACTH) (Harvey *et al.* 1984) by the anterior pituitary (Dickson 1984). In response to ACTH, adrenal cortical activity increases, resulting in increased circulating corticosterone levels within minutes (Beuving and Vonder 1978, Dickson 1984) and increased adrenal cortical mass (Harvey *et al.* 1984) over longer periods of time. Corticosterone is the dominant glucocorticoid in birds (De Roos 1960). Even prior to activation of the HPA axis, however, adrenaline and noradrenaline from the sympathetic neurons and adrenal medulla may already stimulate the release of corticosterone. In this way, stressors such as handling or feed restriction increase adrenal activity (Beuving *et al.* 1989). Stress, however, does not invariably elicit an increase in adrenal activity (Freeman 1985), nor is adrenal activity solely stimulated by stressors. A clear diurnal rhythm of corticosterone levels has been observed in domestic hens (Beuving and Vonder 1977, Johnson and van Tienhoven 1980, 1981). Similarly, it has been suggested that boredom, defined as the absence of stimuli (stimulus = stressor in the broadest sense of the term) in an environment actually causes stress (van Rooijen 1991), and is detrimental to well-being.

Measurements of plasma corticosterone levels have been used extensively as indicators of increased adrenal activity. There are drawbacks, however due to its transience. *In vivo* corticosterone levels are elevated within seconds after the of the induction of stress, and these levels are relatively short-lived, since the presence of free cortisol in the plasma causes immediate negative feedback to the pituitary, which suppresses the release of ACTH (Dickson 1984). Furthermore, sampling for corticosterone actually increases corticosterone. Although sampling techniques generally take this into consideration, serious doubts remain as to the acceptability of corticosterone measurements as an indicator of stress or well-being (Rushen 1991).

Freeman (1985) documents the four most frequently used methods of measuring adrenal cortical activity. They include adrenal mass, the ratio of adrenal cortical mass to medullary mass, decreased adrenal cholesterol concentration, and increased plasma corticosterone. In the short term (hours/days) corticosterone is probably the best measurement of adrenal cortical activity, whereas in the long term, after adaptation has occurred, some measure of adrenal cortical mass would be preferable (Freeman 1985).

The non-specificity of the initial stress response has advantages from a fitness perspective. Prolonged elevation of plasma corticosterone levels causes changes in the production rates of various leukocytes. An increase in heterophil production and inhibition of lymphocyte production have both been observed as a result of elevated plasma corticosterone levels (Gross *et al.* 1980, Gross and Siegel 1983, Davison *et al.* 1983, Maxwell 1993). The decreased lymphocyte production may prevent auto-immunity which would be more likely to occur after prolonged stimulation of specific (as opposed to non-specific) immune factors (Harvey *et al.* 1984).

The differential effect of increased corticosterone levels on hematopoiesis (blood cell development) is a dependable alternative to direct measurements of plasma corticosterone levels. Heterophils

and lymphocytes are illustrated on plate 1. The best indicator of this differential production of leukocytes is an increase in the ratio of heterophils to lymphocytes (Beuving *et al.* 1989, McFarlane and Curtis 1989). Comparison of the heterophil/lymphocyte (H/L) ratio and the corticosterone level as indicators of adrenal function reveals that H/L ratios are more closely correlated with exogenous sources of corticosterone than are plasma corticosterone levels (Gross and Siegel 1983). The H/L ratio is a better indicator than corticosterone concentrations of long-term stress because of the transience of endogenous plasma corticosterone, and because the H/L ratio is the result of the process of white blood cell production, the timing of which is on the order of days rather than minutes.

The effect of feed restriction on the H/L ratio has been measured in chickens. Feed restriction was found to be responsible for an increase in the H/L ratio (Gross and Siegel 1983, 1986). However, chickens are capable of some degree of adaptation, as successive feed deprivations resulted in smaller changes in H/L ratios (Gross and Siegel 1986). Multiple simultaneous stressors act additively to decrease productivity and increase the H/L ratio (McFarlane and Curtis 1989). Maxwell (1993) reviewed the literature regarding changes in the leukocyte population in response to stress, and concluded that heterophilia (an increase in the number of heterophils) may result from mild to moderate stress, but in the case of severe stress, basophilia (an increase in the number of basophils) would be a better stress indicator.

The validity of physiological indicators of stress

There is considerable concern about the validity of the use of physiological indicators to quantify stress in animals. Freeman (1985) suggests that stress does not have a meaningful definition in

Plate 1. Blood cells of the domestic hen. Nucleated erythrocytes (red blood cells) throughout. Lymphocyte (lower left) with large nucleus and light blue cytoplasm; heterophil (upper right) with visible granules in cytoplasm. (magnification 1750x)

biological terms. Physiological responses to stress are difficult to measure, and the application of physiological indicators to quantify stress (or well-being) must be carefully examined (Duncan 1981, Freeman 1985, Rushen 1991). Rushen (1991) points out inconsistencies and surprising conclusions arrived at by questionable use of corticosterone measurements, such as alleviating the stress of tethered sows by further isolating them, and the claim that for laying hens caging is the least stressful form of management. Although the measurements may be valid, the understanding of the biological system is incomplete, and the conclusions may not be valid. Freeman (1985) implies that since adaptations such as increased adrenal activity are tools to increase fitness they will not adversely affect well-being. Natural selection (or genetic fitness) and well-being, however, are totally independent questions.

The question of well-being should focus solely on what an animal feels (Duncan 1990, Curtis and Stricklin 1991, Duncan and Petherick 1991). Attempts to measure animal welfare by physiological means may be premature (Rushen 1991), and any conclusions based on physiological data should be considered with appropriate discretion. Attempts to use measures such as corticosterone levels and H/L levels to measure stress are indirect indicators of stress, and their validity must be interpreted in that perspective.

Stress and animal welfare

Introduction

Animal well-being is difficult to quantify objectively since communication with them is limited to inferences from their behavior. It is useful to consider human well-being not to infer specifically what impacts on animal well-being, but rather to acquire a starting place to make meaningful comparisons. Given the biological similarities between animals and humans, it is not unreasonable to carefully apply general principles pertaining to welfare across species. Care must be practiced, however, because obvious species differences exist (Duncan 1981). The National Wellness Institute (Orlando, Florida) model for human well-being (Ardell and Tager 1981) is widely

accepted (Figure 1). It contains six main elements: physical, spiritual, emotional, social, intellectual, and vocational. All of these elements affect how a person feels. If needs in a single area or element are not met, well-being decreases.

It is apparent that the six element model is unsuitable for the study of animal well-being. Four of the six categories, however, are worthy of consideration. Arguments can be made for the existence of the physical, emotional, social and vocational (broadly defined) aspects of animal life. The intellectual capabilities of animals relative to humans are limited, but exist to some degree. Evidence that environmental enrichment improves well-being and productivity in laying hens (Church 1992) suggests that the vocational / occupational aspect of the NWI model plays a role for animals as well. The intellectual and vocational categories have been combined for animal well-being because of the limited nature of the animal intellect, and because much of the intellectual stimulation seems to come from the environment and leads to various behaviors. The spiritual element has been eliminated, since spirituality on a conscious level is almost certainly not relevant for non-humans. A better animal model would therefore include only four categories, those being physical fitness and nutrition, emotional, social and intellectual aspects (Figure 2).

Overview of related work

The following section contains a brief overview of work that has been done in the area of stress as it applies to animal well-being. It is important to keep in mind the lack of a consistent definition of the concept of stress (Harvey *et al.* 1984) in spite of the many attempts to quantify it. The most general consensus in the literature about the definition of stress is any force influencing an organism which threatens the organism's life, health or well-being.

Figure 1. National Wellness Institute model for human well-being (Ardell and Tager 1981). Each aspect of human existence impacts on well-being. When a challenge or crisis arises in any area well-being is reduced.

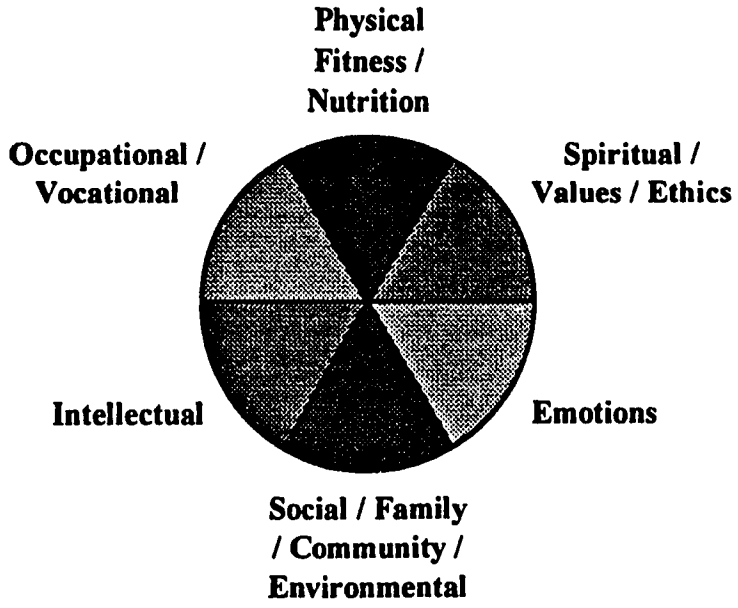
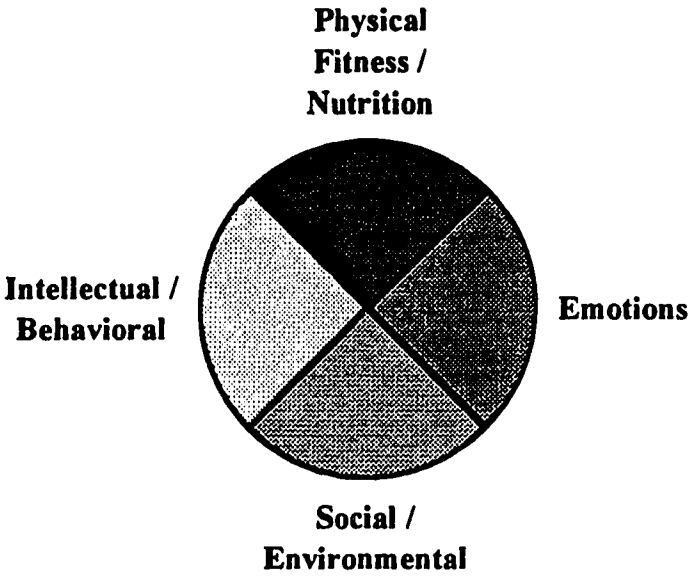


Figure 2. Proposed animal well-being model (modified from Ardell and Tager 1981). As in the model for humans, each aspect of animal existence impacts on well-being. When a challenge or crisis arises in one of the categories well-being is reduced.



Productivity has long been rationalized as an indicator of animal well-being. If an animal's performance is enhanced by a production system, for example, the well-being of the animal was thought to be protected. To some extent this is true, because fitness is generally maximized when conditions for existence are optimal. For example, McFarlane *et al.* (1989) demonstrated that multiple concurrent stressors additively decreased productivity. Applied ethologists, however, argue that an animal's well-being has everything to do with how it "feels". Well-being is not necessarily dependent on an animal's state of health, and is most certainly independent of how productive the animal is (Duncan 1990). There are dangers associated with using productivity as a standard for measuring animal welfare (Duncan 1981), and the concern of animal welfare and animal rights proponents about the association of productivity with well-being (Ripley 1990) is valid .

Possibly the most appropriate model would include a single category: cognitive well-being (Duncan and Petherick 1991). Regardless of the physical state of an animal, if it is unaware of something that negatively affects its welfare, its welfare is not negatively influenced. This is supported by evidence that behaviors normally associated with pain are not necessarily indicative of reduced well-being. For example, in the medical and dental professions anesthetic is used to mask the pain of surgery. In spite of patients writhing or crying out in apparent pain, there is no conscious recollection of the pain afterwards. If an animal's well-being were protected by anesthetic, for example, its actual physical state and any behavioral or physiological indicators normally associated with reduced well-being would be irrelevant (Duncan, unpublished letter). Behavior normally indicative of pain is not necessarily evidence of reduced well-being - only conscious sensation of pain is. Ultimately, cognitive perception of reality, whether real or imagined, is the only parameter that affects well-being. In spite of the merits of the one element

model, it is still useful to break down animal well-being into categories that normally influence well-being.

Specific concerns have been raised about the well-being of broiler breeders subjected to feed restriction (Karunajeewa 1987). Physical stress manifested in the form of hunger pangs due to the absence of feed in the gastrointestinal tract is familiar to humans, and it is likely that animals experience insatiety as well: the ability to sense the need to replenish nutrients is an adaptive response that is certain to increase the fitness of any species through natural selection. The drive to eat is certainly a highly conserved trait.

The increased concern of the poultry industry for animal welfare is a positive step forward. Many animal rights proponents, however, are over-zealous in their attempts to guarantee animal well-being. A compromise can and must be made between the ideal of animal "rights" and animal suffering (Webster 1993). The ideal animal environment is unattainable on a large scale due to political, social, and economic realities. The suffering of fellow humans not only in third-world countries, but next-door to those who have the means to improve their condition demonstrates the problem of misplaced priorities about well-being.

Feed restriction in broiler breeders is exemplary of the need for compromise. It is possible that an animal's short term preference, which is considered to indicate its short term well-being, may conflict with its long-term well-being (Duncan 1992). Feed restriction for broiler breeders is admittedly severe, and attempts to moderate the level of restriction are welcome. However, *ad libitum* feeding also reduces the well-being of a broiler breeder hen. The negative effect of *ad libitum* feed and the trade-off between short-term satiety and long-term physical fitness is analogous in humans. Excessive intake of high nutrient density food may result in increased short-term well-being (satiety), but obesity will likely be the long-term consequence. Conversely,

discipline (insatiety) is required to curtail excess eating. The human dieting industry survives by helping people forego their short-term well-being to maximize their long-term well-being. In the same way, *ad libitum* feed intake in broiler breeder hens results in decreased physical and genetic fitness and possibly decreased well-being in the long-term. The practice of feed restriction may decrease well-being in the short term, but long-term well-being is almost certainly improved.

Nutrient levels play a significant role in the level of obesity that may result from over-consumption. It is possible to maintain a constant nutrient intake while at the same time increase the volume of feed ingested by altering the composition of the diet, and feeding more of it. This strategy optimizes short and long-term well-being, and maintains a reproductively fit bird. In theory, diet dilution with a non-nutritive bulk as a means of qualitative restriction provides an excellent alternative to the current practice of quantitative feed restriction.

Behavioral manifestations of stress

Changes in the frequency of various behavioral patterns, subtle or obvious, seem to be a relatively good indicator of altered well-being in animals. Physical restriction and feed restriction in pigs (Terlouw *et al.* 1991), feed restriction in cattle (Redbo 1990), confinement in horses (Dodman *et al.* 1987) and bank voles (Kennes *et al.* 1988), and feed restriction in chickens (Savory 1989) have been implicated as the cause of stereotypies such as bar biting, tongue rolling, crib-biting, jumping, and spot-pecking. Stress or boredom has been implicated as the cause of these and other stereotypies that play a role in an animal's ability to cope with stressful situations. Wiepkema and associates (1987) found that veal calves which developed stereotyped tongue playing did not develop abomasal ulcers, whereas those calves which did not either had ulcers or scars from ulcers which had healed. Since direct communication is not possible with animals, behavior is likely the best indicator of altered well-being in animals.

Stereotypies are characteristic repetitious activities that serve no apparent purpose. They have been implicated as indicators of reduced well-being. Spot-pecking in feed restricted birds is one such stereotypy. Various explanations of the mechanism responsible for stereotypic behavior have been proposed. Alcock (1984) reports that a baby herring gull instinctively pecks at the red spot on tip of its parent's beak. This stimulates the regurgitation of a meal for the young gull. Spot-pecking is the repeated pecking directed against various items, commonly directed against the feeder, a known source of food. It is possible that spot-pecking represents a vestige of this beak pecking behavior seen in gulls, as it is performed most frequently when food is unavailable.

Another explanation, and one that has received much scientific attention is the claim that endogenous opioids are released as a result of the stereotypical behavior. Savory and associates (1992) injected pullets with nalmefene, an antagonist of central opioid peptide receptors and observed a dose related decrease in spot-pecking. Similar results have been obtained with various mammalian species including crib-biting horses (Dodman *et al.* 1987), normally occurring stereotypies in sows (Cronin *et al.* 1985), and jumping in bank voles (Kennes *et al.* 1988). Stereotypies have actually been induced in mice by a dopamine agonist (Kennes *et al.* 1988). Since spot-pecking may be associated with the central release of endogenous opioids, it may function as a means of coping with stress. There is evidence that opioids may play a greater role in young animals (Kennes *et al.* 1988) or in the early stages of the development of stereotypies (Cronin *et al.* 1985).

Alternatives to quantitative feed restriction

Previous studies

In spite of the merits of feed restriction, there are drawbacks associated with the widespread practice of quantitative restriction. Standard levels of feed restriction are quite severe. During rearing, broiler breeder pullets are fed 60% (Yu *et al.* 1992b, Hocking 1993) to 70 or 80% less than *ad libitum* (Karunajeewa 1987) and 25 to 50% less than *ad libitum* fed birds during lay (Yu

et al. 1992b). The occurrence of mouth-based stereotypies such as spot-pecking (Savory 1989), aggressive behaviors (Bennet and Leeson 1989), and the tendency of feed restricted birds to consume higher quantities of water (Savory 1989) have led to the conclusion that the welfare of these birds is negatively affected by the hunger imposed by feed restriction.

Feed restriction is necessary to maintain productivity in broiler breeders. Control of food intake may ultimately be possible by direct or indirect manipulation of the brain and neurotransmitters (Kuenzel 1989, Snapir and Robinzon 1989). Manipulation of the hypothalamus has altered feeding behavior. For example, ventromedial lesions of the hypothalamus cause hyperphagia, and lateral lesions cause a complete withdrawal from feeding activity (Duke 1984). Currently, however, physical restriction of feed is the only practical option. There has been much study of the practice of quantitative feed restriction (reviewed by Robinson et al. 1993), and considerable study of qualitative feed restriction (Leeson and Summers 1991). Qualitative feed restriction by definition is the dilution of one or more essential ingredients in the diet, thereby increasing the intake required to maintain productivity at the same level. Karunajeewa (1987) reports that low protein diets fed in higher quantities did not adversely affect immunological development, delay sexual maturity, or decrease productivity in broiler breeder hens.

Effects of fiber on digestion

There is evidence that cellulose can cause a depression in protein, starch and lipid digestibility. The hulls from field beans depress protein and starch digestion by adsorbing digestive enzymes onto the indigestible substrate and thus inhibiting the action of the enzymes (Longstaff *et al.* 1991, Longstaff and McNab 1991). This reduction in digestibility is highly pronounced when condensed tannins are present in the hulls. Tannin enzyme complexes were found to tie up dietary enzymes for protein, starch and lipid digestion in chicks (Longstaff and McNab 1991). Reduced digestibility resulting from high levels of fiber suggest that exceedingly high levels of fiber in the diet may have a negative effect on the productivity of an egg laying hen. Turnover of protein and

lipid during egg formation is very high, and as a result the hen is in need of an adequate source of these nutrients. If nutrient dilution is too severe, nutrients or digestive enzymes will be tied up by the fiber or by tannins. In spite of *ad libitum* intake of high fiber diets, nutrient requirements may not be met, and decreased productivity may result.

Diets designed for *ad libitum* intake by the addition of high levels of fiber have resulted in decreased egg production and egg weight compared to full-fed and restricted feeding regimes (McKay 1980) in spite of the maintenance of target BW. McKay (1980) suggested that fiber decreases the ability of the pullet to utilize calcium and fats. McKay (1980) also found that liver size was significantly reduced in pullets fed high levels of fiber. Although the mechanism for this reduction in performance is unclear, the decrease in liver size may indicate a reduced ability to metabolize lipids and this may have led to the decrease in subsequent performance.

The choice of fiber to be used as a diluent may be important. Fibers with low tannin content were found to depress protein, starch and lipid digestibility, but to a relatively small extent compared to tannin rich fibers (Longstaff *et al.* 1991). Fibers with a low tannin content are probably a better choice for diluting poultry diets.

Implications of diet dilution for broiler breeders

Diet dilution, or qualitative feed restriction is a logical solution to the problem of stress associated with feed restriction, and has been proposed by animal welfarists (Duncan 1990). There are a few drawbacks with the use of diluted diets. From a practical point of view, the bulkiness of diluted diets makes the feed more labor intensive to handle and more expensive to transport and store. The volume of manure may also be increased. This may be problematic especially in regions of dense human population, where waste management is already a significant issue. Secondly, the anti-nutritive properties of substances such as tannins (which are often found in close association with cellulose) may counteract any benefits that may be gained from diet dilution. The choice of a

quality fiber is very important. Fiber availability and consequent quality control of the diet must also be considered. Advantages of qualitative feed restriction include the potential improvement in the well-being of the birds, and metabolic stasis that may lead to improvements in productivity. Since the cost of fiber is presently very low, there may be economic benefits in the utilization of fiber as a diluent in broiler breeder rations. A comprehensive economic analysis, which is not the goal of this thesis, is necessary to determine the economic viability of nutrient dilution for the broiler breeder industry.

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Chapter 2 - The effect of nutrient dilution on the well-being and performance of female broiler breeders

The problem

The practice of feed restriction in broiler breeders has received attention from an animal welfare perspective (Karunajeewa 1987). Mouth based stereotypies such as spot-pecking are commonly performed by feed restricted pullets and hens, and are thought to serve as coping mechanisms to alleviate the stress of feed restriction (Savory 1989, Savory *et al.* 1992). Aggressive behaviors such as feather pecking, the tendency of feed restricted birds to consume higher quantities of water (Savory 1989), and reported changes in heterophil to lymphocyte (H/L) ratios in feed restricted broiler breeders (Gross and Siegel 1983, 1986) have led to the conclusion that the welfare of these birds is negatively affected.

There are two practical means of restricting nutritive intake: one is quantitative feed restriction, which currently is most widely practiced, and the second is qualitative feed restriction. In order to maximize productivity, feed allotments to broiler breeders are commonly restricted at a level of 60% to 80% less than *ad libitum* fed birds during rearing (Karunajeewa 1987, Yu *et al.* 1992a, Hocking 1993) and 25% to 50% less than *ad libitum* during the laying period (Yu *et al.* 1992a). Compared to *ad libitum* fed birds, feed restricted broiler breeders show increased egg production (Robinson 1991, Yu *et al.* 1992b, Robinson *et al.* 1993a), increased persistency of lay (Fattori *et al.* 1991), longer laying sequences (Robinson *et al.* 1991), fewer eggs laid outside the normal time of oviposition (Yu *et al.* 1992b), fewer defective eggs, and fewer multiple ovulations in a single day (Fattori *et al.* 1991, Yu *et al.* 1992b).

Qualitative feed restriction involves the dilution of feed with non-nutritive bulk or reformulation of diets to achieve lower concentrations of dietary protein and energy. Although altered concentrations of dietary protein and energy have been widely studied, most studies involve the

alteration of either one amino acid or the level of protein or dietary energy singly, while holding the rest of the diet constant. Diluted diets have been formulated for *ad libitum* intake (McKay 1980), but there has been little or no attempt to determine the quantity of fiber addition that may optimize broiler breeder well-being and productivity.

Objectives

The objectives of this study were:

1. to determine whether nutrient dilution would extend the period of time required for broiler breeder females to consume a daily ration of feed.
2. to quantify physiological manifestations of stress in broiler breeder females during both rearing and laying by measuring the ratio of heterophils to lymphocytes (H/L).
3. to quantify behavioral manifestations of stress in the broiler breeder female during both rearing and laying. Indicators of stress included: stereotypical coping behavior (spot-pecking), aggression, and time spent at the water supply.
4. to relate physiological and behavioral manifestations of stress with the level of qualitative diet dilution.
5. to determine whether qualitative restriction with quantitative feed restriction improves broiler breeder well-being compared to quantitative feed restriction alone.
6. to determine whether diet dilution has an effect on subsequent reproductive performance of the broiler breeder female. Indicators of reproductive performance included:
    - hen-day egg production
    - fertility
    - hatchability
    - egg shell quality
    - egg weight

7. to determine whether diet dilution has an effect on subsequent flock characteristics. Characteristics of importance included:
    - flock uniformity
    - feed efficiency
    - mortality

Hypotheses

The hypotheses regarding the outcome of the study were as follows:

1. Nutrient dilution would significantly extend the daily period of time in which feed is available to the birds. This extension would have a positive linear relationship with the level of dilution.
2. If the time taken to consume the feed increased, the competitive edge of the more aggressive birds would be reduced. Diet dilution would then result in more even feed distribution which in turn may result in improved flock uniformity.
3. Feed restriction is a stressor of sufficient potency to alter H/L ratios. Nutrient dilution would alleviate this stress to some extent, and as a result H/L ratios would be lower in diluted rations than in more concentrated rations.
4. Stereotypical behaviors such as feeder directed spot-pecking, aggressive behavior, and time spent at the drinker have been associated with feed restriction stress. These indicators were therefore expected to be manifested in the Control (undiluted) treatment. Insatiety may be relieved by nutrient dilution. As a result, the frequency of spot-pecking, drinking, and aggressive behavior would be reduced in birds fed diluted rations.
5. The H/L ratio and the behavioral manifestations of feed restriction stress would be related in a linear fashion to the level of qualitative diet dilution, indicating that well-being had improved.
6. The performance of the birds may be positively correlated with improved well-being. Therefore egg production, fertility, hatchability, egg weight and egg quality were monitored for changes.

7. Other parameters such as feed efficiency and mortality may also be affected by nutrient dilution.

The experiment (materials and methods)

The rearing phase

Stock, housing, and management

Four hundred and eighty SHAVER broiler breeder pullets were individually weighed and wing banded at one day of age. They were randomly placed, 80 per pen, into six floor pens (see figure 3) measuring 4.31 x 4.92 m (14' x 16') in a light-tight facility. Removable pit-type roosts covered 1/3 of the floor area, and were in place from 3 weeks of age to the end of the rearing period. The pullets were exposed to a standard photoschedule of 23L:1D for the first three days, and 8L:16D from 3 days to 20 weeks. Wheat straw was used for bedding.

Feed allocation

Three restrictive dietary treatments were imposed for the entire study period (rearing and laying). The Control group of birds was fed standard rations appropriate for the age of the birds. The primary ingredients of the rearing rations were wheat, barley, and soy meal (Appendices 1-3). Two levels of diet dilution were also imposed, by adding 15 kg (D15) and 30 kg (D30) of ground oat hulls to 85 and 70 kg of the standard (Control) diet, respectively (table 1). All birds were fed the starter diet *ad libitum* for the first 3 wk. For the entire rearing period after 3 wk, a daily feed restriction regime was implemented. All diets were fed at a level so as to achieve the breeder's recommended body weights (BW). The daily feed allotment was calculated for each pen individually, based on the mean BW of the pen, the breeder's recommended BW and the breeder's recommended feed allocations. Water was supplied *ad libitum* throughout the rearing period.

Figure 3. Experimental Design. Three treatment groups were maintained for a 56 week study period. 160 pullets per treatment were reared in two floor pens from 0 to 22 weeks of age. At 22 weeks of age, 80 pullets per treatment were randomly placed in cages in a separate facility with another bird from the same treatment. The remaining pullets were kept in floor pens for the egg production period.

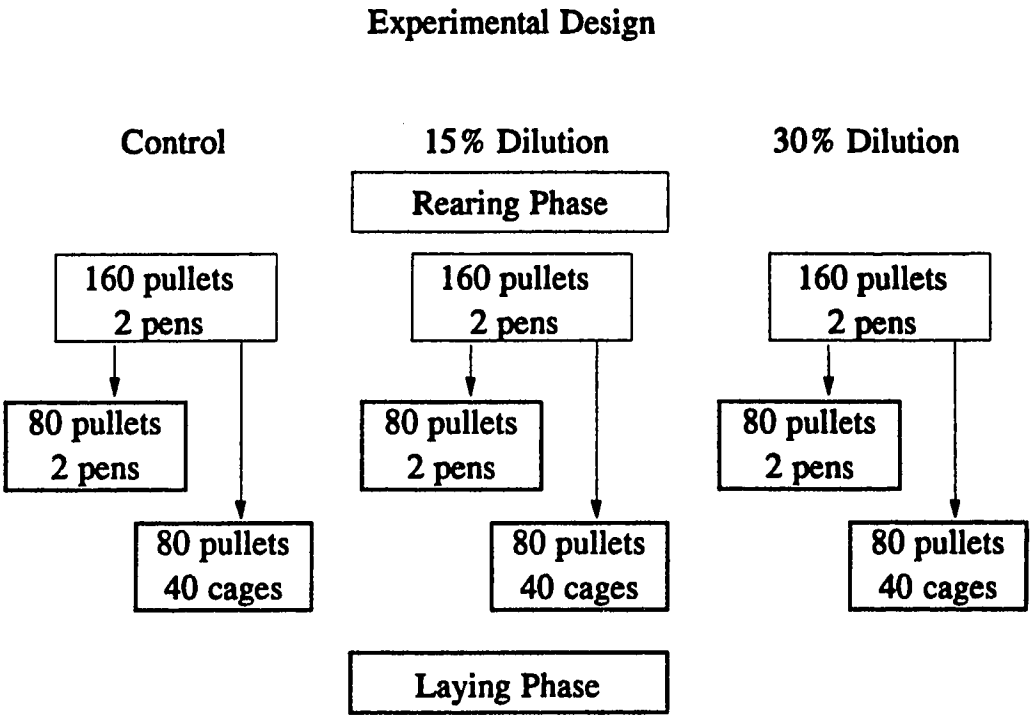


Table 1. Nutrient dilution levels implemented from 0 to 56 wk.

Treatment	Control	D15	D30
Feed (kg)	100	85	70
Ground Oat Hulls (kg)	0	15	30
Level of Dilution (% hulls in diet)	None	15%	30%

Proximate analyses was performed on the starter and grower rations. Calculated and actual analyses of these rations are given in table 2 and table 3. The calculated analysis for the pre-breeder ration is given in table 4. Proximate analysis was also performed on the diluent, ground oat hulls. The results of this analysis are shown in table 5.

Body weights

The pullets were individually weighed at 2, 4, 8, 12, 16, and 20 weeks of age (table 6). Group weights were taken at 6, 10, 14, and 18 weeks for the purpose of calculating feed allocation. Feed consumption rates were monitored twice weekly from 4 to 20 weeks of age by estimating the time at which the last feed disappeared from the feeders.

Flock uniformity for the rearing period was calculated using the individual weights of all the birds in each pen. The percentage of birds within each pen with body weights within 15% of the mean pen BW was calculated (traditional method). More recently, the coefficient of variation (CV) has been used to indicate the degree of variability in BW. Since from a statistical point of view the CV is a more meaningful indicator than the traditional method of calculating flock uniformity, the CV is reported with all body weights. Both are presented for purposes of comparison.

Measurements of stress

Heterophil/lymphocyte ratio

At 12 and 20 weeks of age, 40 birds from each pen were randomly selected. Five drops of blood were collected with a capillary tube from the brachial vein, and blood smears were made on duplicate glass slides. These smears were stained with Wright-Giemsa stain, and a total of 50 leukocytes (only heterophils and lymphocytes) were counted on each slide. At 12 weeks of age, the H/L ratio was calculated for at least 20 pullets per pen. The ratio of heterophils and

Table 2. Calculated composition and actual analysis of broiler breeder starter ration on a dry matter basis. Ration fed *ad libitum* from 0 to 3 wk. Calculations based on the contribution of both the feed and the oat hulls.

Treatment	Control		D15		D30	
	Calc	Actual	Calc	Actual	Calc	Actual
ME (kcal/kg)	2739	*	2328	*	1917	*
Crude protein (%)	19.1	18.4	16.9	16.5	14.8	14.4
Calcium (%)	0.90	0.80	0.81	0.61	0.73	0.65
Total phosphorus (%)	0.72	0.63	0.63	0.51	0.54	0.44
Acid detergent fiber (%)		4.1		9.7		13.3

* Not measured.

Table 3. Calculated and actual analysis of broiler breeder grower ration on a dry matter basis. Ration fed from 3 to 14 wk. Calculations based on the contribution of both the feed and the oat hulls.

Treatment	Control		D15		D30	
	Calc	Actual	Calc	Actual	Calc	Actual
ME (kcal/kg)	2811	*	2389	*	1968	*
Crude protein (%)	15.5	17.7	13.9	15.1	12.3	12.2
Calcium (%)	0.86	1.01	0.78	0.80	0.70	0.74
Total phosphorus (%)	0.61	0.71	0.54	0.59	0.46	0.46
Acid detergent fiber (%)		5.8		11.5		16.3

* Not measured.

Table 4. Calculated composition of pre-layer broiler breeder ration on a dry matter basis. Ration fed from 14 to 20 wk. Calculations based on the contribution of both the feed and the oat hulls.

Treatment	Control	D15	D30
	Calc	Calc	Calc
ME (kcal/kg)	2772	2356	1940
Crude protein (%)	14.6	13.1	11.6
Calcium (%)	0.76	0.70	0.63
Total phosphorus (%)	0.60	0.53	0.45

Table 5. Proximate analysis of ground oat hulls on a dry matter basis.

	Analysis
Crude protein (%)	4.7
Calcium (%)	0.33
Total phosphorus (%)	0.11
Acid detergent fiber (%)	35.8

Table 6. Rearing body weights of feed restricted broiler breeder females fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	BW (g)	n [2]	CV [1]	BW (g)	n	CV [1]	BW (g)	n	CV [1]
0	35.0	162	8.4	34.9	163	8.2	35.1	163	8.2
2	166.2	162	20.4	165.5	164	21.8	163.2	160	19.4
4	390.4	156	15.3	408.3	152	14.1	399.8	153	14.0
8	790.9	155	16.3	814.7	152	16.3	831.4	153	13.8
12	1211.6	155	16.6	1248.5	152	15.0	1251.9	153	14.5
16	1589.1	154	16.8	1680.1	152	15.6	1655.8	152	14.3
20	2091.7	153	13.6	2129.5	152	14.8	2154.1	152	14.0
22	2269.0	153	14.6	2320.6	151	14.2	2330.4	152	14.0

1 Coefficient of variation.

2 Individual birds within treatment.

lymphocytes was calculated by dividing the number of heterophils by the number of lymphocytes. At 20 weeks of age, the H/L ratio was determined for three pullets per pen.

A seventh pen of pullets from the same hatch was fed the Control diet *ad libitum* in the same facility for the entire rearing period. At 12 weeks blood smears were collected from these birds, to compare H/L ratios between birds in the experimental treatments and full-fed birds. Although not part of the statistical design, the H/L ratio of the full fed birds is presented to facilitate a comparison with satiated pullets.

Behavior

Each of the six pens of eighty pullets was videotaped at 8, 16, and 20 weeks of age. A Panasonic CCTV camera (model WV-1410) with a 12.5-75 mm zoom lens was used, and the image was recorded on videotape with a Panasonic time lapse video cassette recorder (model AG-6720A). The camera was suspended from the ceiling and faced the end of the pen which contained the drinkers. Each pen was allowed to readjust for 5 minutes after being disturbed during the placement of the camera. Continuous videotape was then collected for a period of 10 minutes.

The following categories were used to classify the behavior of the pullets:

1. Resting: any bird which was lying down or perched with its head in a tucked position.
2. Eating: any bird actively eating or searching the feeder for feed.
3. Drinking: any bird drinking or pecking at the drinker.
4. Spot-pecking (feeder): Any bird actively engaged in stereotypical spot-pecking (>3 pecks) and which was directed at the feeder.
5. Spot-pecking (other): Any birds which pecked repeatedly (>3 pecks) at a surface other than the feeder.
6. Preening: any bird which was grooming.

The scan time sampling method (Lehner 1992) was used to determine the numbers of all observable pullets engaged in the various behaviors. For the 10 minute counting period, each bird

which was engaged in one of these behaviors at 1 minute intervals (as indicated by a time stamp on the videotape) was counted. The counts represent the total number of all birds within a pen engaged in a given behavior.

Mortality

All mortality was recorded for the rearing and laying periods in floor pens and in cages. Post-mortem analysis was performed by a veterinarian to determine the cause of death.

The laying phase

Housing and management

At 20 weeks of age, all of the pullets were photostimulated by adjusting the photoschedule to 14L:10D. This photoschedule was maintained for the duration of the study. An undiluted (Control) laying ration (Appendix 4), and the same levels of dilution used during rearing (table 1) were continued for the entire laying period. Proximate analysis of a sample of the layer diet fed to each treatment group is given in table 7. Feed was supplied daily at a level at which breeder recommended BW would be maintained.

Caged breeders

At 22 weeks of age 240 pullets (80/treatment) were moved to 120 Cage Master B.E.C. cages (Cominex International Inc., Brantford, ON) measuring 51 x 46 cm (18" x 20") in a light-tight facility. Equal numbers of pullets (40) from each rearing pen were placed randomly into cages (see figure 3) with another pullet from the same treatment. Trough feeders on the fronts of the cages were sub-divided so that no feed could be consumed by birds in neighboring cages. The hens were housed two per cage from 22 weeks to 56 weeks of age. Treatments were randomly arranged, and blocks of 10 cages of the same treatment were grouped to facilitate egg collection in lots for the hatchery. Five of the 10 cages per block were in the top tier and the remaining five were directly underneath in the bottom tier. This was done to balance any effect of differential light or other environmental differences due to the tier that may have had an effect on

Table 7. Calculated and actual analysis of broiler breeder laying ration on a dry matter basis. Ration fed from 20 to 56 wk. Calculations based on the contribution of both the feed and the oat hulls.

Treatment	Control		D15		D30	
	Calc	Actual	Calc	Actual	Calc	Actual
ME (kcal/kg)	2738	*	2327	*	1917	*
Crude protein (%)	16.3	17.6	14.6	15.9	12.8	15.0
Calcium (%)	3.46	1.71	2.99	2.63	2.52	2.49
Total phosphorus (%)	0.66	0.50	0.58	0.56	0.50	0.60
Acid detergent fiber (%)		3.3		7.2		9.4

* Not measured.

productivity or well-being. Lights in the caging facility came on at 0300h daily. This provision allowed for most of the eggs to be cleared from the oviduct by the time of artificial insemination. Birds were weighed every second week (table 8). Every 7 days all of the hens were artificially inseminated with approximately 40 µL of fresh semen. Semen was collected from SHAVER broiler breeder males (same age flock) housed in cages in the same facility, and pooled. Pooled semen was used within 30 minutes of collection.

Daily feed allocations were provided at 0800h (or 1100h on days when the birds were weighed). The average BW of all birds in each treatment, the breeder's recommended BW, and the breeder's recommended feed allocation were considered in the calculation of the feed allocation for each subsequent 2 wk period. Feed allocation calculations were reduced by 5% for caged birds to compensate for decreased activity levels. All of the cages in each treatment received the same allotment of feed. Because of water wastage, water was withheld daily for 4 hours from 1200h to 1600h from 22 to 26 wk. *Ad libitum* access to water was restored from 28 wk to the end of the study.

Floor pens

The remaining pullets not moved to cages were kept in floor pens measuring 4.31 x 4.92 m (14' x 16') from 22 to 47 weeks of age, at which time the floor pen study was terminated. Lights came on at 0600h daily. Daily feed restriction at the same levels of dilution was continued, with feed supplied at 0730h daily. Roosters were placed with the hens at a ratio of 1:8, respectively. Chore-Time sex-separate feeders were used to facilitate gender separate feeding, thus ensuring the correct feed allotment for the female breeders. Individual body weights were measured every 4 wk (table 9). Group BW were measured bi-weekly for the purpose of calculating feed allocation. Feed allocation was calculated on an individual pen basis, as opposed to a treatment basis for the caged birds. Water in the floor pens was supplied *ad libitum* for the entire laying period.

Table 8. Body weights of feed restricted broiler breeder females which were caged during the laying period and which survived to 56 weeks and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	BW (g)	n [2]	CV [1]	BW (g)	n	CV	BW (g)	n	CV
0	34.6	73	7.6	34.9	71	8.1	34.9	64	7.6
2	168.6	79	15.3	174.6	79	13.6	168.2	76	12.2
4	392.3	79	13.4	414.3	79	13.1	399.9	76	12.3
8	784.0	79	14.5	836.0	79	14.8	839.4	76	11.5
12	1203.6	79	15.5	1269.3	79	16.0	1274.2	76	12.9
16	1592.3	79	14.8	1690.1	79	17.2	1675.5	76	13.5
20	2079.6	79	12.7	2128.5	77	16.4	2172.9	76	13.2
22	2267.4	79	12.1	2328.4	77	15.9	2360.8	76	13.4
24	2547.8	79	10.4	2612.4	79	13.4	2633.5	76	10.6
26	2813.9	79	9.9	2853.2	79	10.8	2900.4	76	9.5
28	2989.4	79	9.6	3059.2	79	10.3	3004.7	76	9.5
30	3145.4	79	9.5	3223.8	79	9.9	3199.4	76	9.0
32	3208.9	79	10.6	3326.9	79	10.2	3279.4	76	9.1
34	3284.7	79	11.0	3374.8	79	10.5	3358.2	76	9.4
36	3377.7	79	11.1	3436.5	79	10.7	3447.3	76	9.6
38	3430.3	79	11.4	3482.0	79	10.9	3475.5	76	9.6
40	3468.1	79	12.1	3525.9	79	10.9	3556.3	76	9.6
42	3515.1	79	12.2	3573.6	79	11.3	3651.3	76	9.7
44	3549.9	79	13.0	3609.9	79	11.6	3660.9	76	10.0
46	3561.9	79	13.2	3614.9	79	11.7	3704.3	76	10.0
48	3573.3	79	13.6	3619.5	79	12.0	3747.1	76	10.2
50	3537.2	79	14.0	3585.2	79	12.1	3752.2	76	10.4
52	3507.6	79	14.9	3578.3	79	12.3	3714	76	10.7
54	3540.0	79	15.0	3570.2	79	12.4	3747.8	76	10.6
56	3539.3	79	14.8	3585.4	79	12.9	3706.8	76	11.1

1 Coefficient of variation.

2 Individual birds within treatment "n" is smaller at placement because lost wing bands made tracing of original BW impossible.

Table 9. Average laying period body weights of feed restricted broiler breeder females housed in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age(wk)	BW (g)	n [1]	CV	BW (g)	n	CV	BW (g)	n	CV
26	2758.4	71	11.3	2817.5	65	9.6	2844.7	68	13.2
30	3059.8	71	10.4	3119.8	65	11.5	3221.5	68	11.8
34	3131.6	71	10.8	3346.3	65	12.2	3217.8	68	11.0
38	3291.6	71	9.5	3367.0	65	10.4	3363.2	68	10.7
42	3407.9	71	10.4	3497.6	65	11.5	3484.8	67	9.7
47	3356.1	71	10.5	3433.7	65	12.1	3485.9	68	15.9

[1] Individual birds within treatment.

Rate of feed consumption

The rate of feed consumption was calculated for the caged hens twice a week for eight consecutive weeks (34-41 wk of age). The time of feed disappearance for each cage was recorded. When not all of the feed was consumed in a 24 hour period, feed disappearance times were estimated. The average amount of feed consumed between 1630h and 0800h was calculated for birds with feed left over. This average feed consumption was assumed to be representative of the quantity consumed by all of the birds

which had feed left over. The consumption of this feed was assumed to have taken place at a linear rate and only during the hours of light. An estimated time of feed disappearance was then calculated for those cages in which feed had been completely consumed by morning.

Total egg production

Eggs were collected daily at 1300h. Egg production in cages was monitored daily on an individual cage basis (n=120) from 22-56 weeks, and on a pen basis (n=6) in floor pens. The incidence of normal, double yolked, soft-shelled, shell-less, misshapen eggs, eggs broken during handling, and eggs pecked by the hens were recorded for caged birds, and total egg production was recorded for floor birds. Egg weights were recorded once weekly for caged birds. For the caged birds the onset of production was estimated by the age at 50% production (first egg in each cage). In order to compare productivity as a function of BW and flock uniformity, the birds were sorted on the basis of both BW and flock uniformity. The BW and flock uniformity ranges were divided into three equal categories, and the average egg production of the birds falling into the nine combined categories was calculated. The weighted average for each flock uniformity and BW category was also calculated.

Hatchability and fertility

All eggs from weeks 28 to 56, with the exception of weeks 45, 46, 48 and 49 were sent to a commercial hatchery (Lilydale Cooperatives Ltd., Edmonton, Alberta) for incubation and hatching. Residues from the hatchery were examined to distinguish fertile from infertile eggs.

Flock uniformity and efficiency

Flock uniformity for the laying period was calculated for those cages (n=112) housing two hens for the entire production period. Cages in which one bird died were not included in the calculation because the intention of the calculation was to determine the effect of diet dilution on competition and thereby the effect of diet dilution on flock uniformity. For the caged birds, the CV was calculated using lots (groups of 10 cages) as "flocks". In the floor pens, flock uniformity was calculated on a pen basis. Flock uniformity was calculated as:

1. the percentage of birds with a BW within ±15% of the mean flock weight, and
2. the coefficient of variation.

Measurement of stress

Behavioral and physiological indicators of stress were investigated to determine the effect of nutrient dilution on the well-being of the hens during the laying period. Behavioral measurements were done at 46 wk of age on the birds in the floor pens, and the H/L ratio was assessed in the caged birds at 54 wk.

Heterophil/lymphocyte ratio (cages)

At 54 weeks of age a capillary tube of blood was collected from the brachial vein of a single bird from each cage (n=120). Duplicate smears were made on microscope slides for each bird. A single slide from each bird was stained with Wright-Giemsa stain and 50 leukocytes (only heterophils and lymphocytes) were counted on each slide. The H/L ratio was calculated by dividing the number of heterophils by the number of lymphocytes counted.

Behavior (floor pens)

At 46 weeks of age, the behavior of the hens in floor pens was monitored. Two of the four feeders in each of the treatment rooms were within the field of view and were recorded on the videotape. One frame was recorded per minute for a 24 hour period. Since the photoschedule was 14L:10D, approximately 840 (60 min./hr x14 hr of light) frames were recorded per pen. The scan time sampling method (Lehner 1992) was used to determine the number of all observable individuals within each pen which were engaged in various activities at specific points in time (each frame, which was separated by 60 seconds). The treatments that were monitored were

1. Control	2 pens for 24 hr/pen
2. D15	2 pens for 24 hr/pen
3. D30	2 pens for 24 hr/pen
4. Full fed (Control ration fed *ad libitum*)	1 pen for 48 hr

The following behaviors were monitored:

1. Resting: any bird lying down.
2. Eating: any bird with its head inside of feeder.
3. Drinking: any bird standing at the drinker with its head near the drinker.
4. Spot-pecking: any bird with its head within striking distance of the feeder.
5. Aggressive behavior: feather pecking, threatening posture or behavior, or physical contact.
6. Dust bathing: any bird lying on the floor which appeared to be rolling in the litter.

Statistical analysis

Data collected during the rearing period were analyzed as completely random design. Sources of variation were treatment, age, and tier. Body weights, feed consumption, feed consumption rate, feed conversion efficiency, H/L ratios, behavior data, egg weights, egg production, flock uniformity, fertility and hatchability data were analyzed by means of either 2 or 3 way analysis of variance (ANOVA). Because of diurnal patterns in behavior, time of day was considered a source of variation in behavioral analyses. The General Linear Models (GLM) procedure in SAS (1989)

was used. Since the tier effect was not significant in any calculations, it was ignored, and no discussion of the tier effect is present in this study. Where significant treatment effects were found, differences between treatment means were determined using the least significance difference test (SAS 1989). Eggs from weeks 28 to 37 (early), 38 to 44 (mid production), and 45 to the end of the study (56 wk in cages; 47 wk in floor pens) (late) were pooled for analysis of variance. Percentage data (fertility, hatchability, and mortality data) were transformed with the arcsine (angular) transformation (*e.g.* $\theta = \arcsin\sqrt{fertility}$) (Sokal and Rohlf 1981, p.427) to achieve a more normal distribution of the data prior to analysis of variance. Both transformed and untransformed data were submitted for ANOVA (SAS 1989). The data and SEM presented in the tables of fertility, hatchability, and mortality is untransformed, however, the levels of significance are from the results of the ANOVA using the transformed data. Regression analysis (SAS 1989) was performed on the CV data from 26 weeks of age (start of production) to the end of the trial for birds in floor pens and in cages to analyze temporal trends in flock variability resulting from the experimental treatments. Efficiency was calculated as the amount of feed (feed efficiency) and as the amount of CP (CP efficiency) required to achieve various measures of productivity. Since there was not an accurate estimate of metabolizable energy (ME) in the diets, ME efficiency was not calculated. Feed efficiency data were subjected to χ^2 test of goodness of fit (Sokal and Rohlf 1981, p.703) to determine whether feed efficiency in the treatments was different from that which was expected.

In the floor pens, the pen was considered to be the experimental unit for all analyses, with one exception. The H/L ratio was analyzed using the individual bird as the experimental unit. The use of individual birds as the experimental unit when a treatment is applied to the pen is an accepted practice in the determination of H/L ratios in feed restricted hens (Gross and Siegel 1983, 1986, Savory 1989, Maxwell *et al.* 1992). Individual cages served as the experimental unit for the caged breeder hens with the exception of hatchability data and flock uniformity calculations. Since the

eggs from blocks of birds were hatched together in lots, blocks of 10 cages were used as the experimental unit. Because of the artificial nature of a two bird flock (flock = cage), 4 blocks of 10 cages (20 birds) for each treatment were treated as flocks for flock uniformity calculations.

Results and discussion

Feed consumption

The amount of feed consumed differed between treatments for both the rearing (table 10) and laying periods (table 11). The D15 and D30 treatments were expected to consume approximately 15% and 30% more feed than the Control treatment, respectively, based on the assumption that the ground oat hulls were completely non-nutritive. Total feed consumption for the rearing period was lower than expected in the D15 and D30 treatments (table 10), indicating that ground oat hulls may have some minor nutritive contribution for pullets. In the laying period, the difference in total feed consumption from expected was even lower in the D15 and D30 treatments than during the rearing period (decreased from 113.3% to 110.3% in the D15 treatment; 126.9% to 125.1% in the D30 treatment; table 10 and table 11), indicating that there may be a greater nutritive contribution by the oat hulls during the laying period. This may be due to increased enzymatic development in adult breeder hens. Similar ratios were found in the birds which were caged during the laying period (110.7% of Control in D15; 121.2% of Control in D30; table 12). Less feed (relative to Control) was consumed by the caged D30 birds than the penned D30 birds, which may be a function of the egg productivity (see table 25); egg production was significantly higher in the D15 treatment than the D30 treatment in the caged birds, but not in the floor pens.

Time to consume feed

The difference in feed consumption rates is the basis for the hypothesis that qualitative feed restriction will reduce the stress of feed restriction in female broiler breeders. The time required

Table 10. Allocation of a commercial ration undiluted and diluted at two levels with ground oat hulls by feed restricted broiler breeders housed in floor pens during the rearing period.

Treatment	Control			D15			D30		
Age (wk)	feed (g) bird.day	SEM [1]	CP (g) bird.day	feed (g) bird.day	SEM [1]	CP (g) bird.day	feed (g) bird.day	SEM [1]	CP (g) bird.day
0.0	13.1	0.1	2.41	12.6	0.3	2.08	12.0	0.1	1.73
1.1	23.6	0.7	4.34	23.7	0.2	3.91	23.6	0.5	3.40
2.1	30.0^{a}	0.0	5.52	34.5^{b}	0.0	5.69	38.7^{c}	0.2	5.57
3.1	53.9^{a}	0.1	9.54	63.6^{b}	1.0	9.60	66.5^{b}	0.8	8.11
3.4	39.5^{a}	0.0	6.99	58.7^{b}	0.8	8.86	69.5^{c}	1.1	8.48
3.6	43.6^{a}	0.1	7.72	52.5^{b}	0.6	7.93	52.8^{b}	0.8	6.44
4.3	42.2^{a}	1.8	7.47	50.0^{b}	0.3	7.55	57.2^{c}	0.3	6.98
5.3	47.3^{a}	0.7	8.37	53.5^{b}	0.3	8.08	61.0^{c}	0.6	7.44
6.3	51.9^{a}	0.8	9.19	57.8^{b}	1.0	8.73	66.2^{c}	0.6	8.08
7.3	51.5^{a}	1.8	9.12	61.0^{b}	1.7	9.21	67.4^{b}	0.2	8.22
8.3	57.6^{a}	0.1	10.20	65.2^{b}	0.9	9.85	71.7^{c}	0.2	8.75
9.3	58.7	2.2	10.39	63.8	1.0	9.63	71.1	2.0	8.67
10.3	58.5^{a}	2.0	10.35	69.0^{a}	1.4	10.42	78.5^{b}	2.9	9.58
11.3	65.6^{a}	0.7	11.61	70.6^{a}	0.5	10.66	82.5^{b}	2.1	10.07
12.4	68.1^{a}	0.0	12.05	77.1^{b}	1.1	11.64	85.5^{c}	0.1	10.43
13.3	70.6^{a}	0.3	12.50	81.7^{b}	0.3	12.34	92.3^{c}	0.2	11.32
14.3	76.2^{a}	0.4	11.13	88.1^{b}	2.0	11.54	99.1^{c}	1.7	11.50
15.3	79.2^{a}	1.1	11.56	91.1^{b}	2.4	11.93	101.7^{b}	1.5	11.80
16.3	85.4^{a}	0.1	12.47	94.4^{b}	0.3	12.37	107.0^{c}	0.3	12.41
17.3	91.4^{a}	1.2	13.34	98.0^{a}	0.7	12.84	115.8^{b}	2.3	13.43
18.3	95.0^{a}	1.9	13.87	107.3^{b}	2.0	14.06	121.3^{c}	1.3	14.07
19.3	99.9^{a}	0.3	14.59	116.2^{b}	1.3	15.22	128.3^{c}	0.5	14.88
20.6	101.9^{a}	0.4	14.88	115.7^{b}	0.8	15.16	128.4^{c}	0.4	14.89
Rearing Total (g/bird) (% of Control)	9866^{a} (100)	20	1635	11179^{b} (113.3)	38	1626	12523^{c} (126.9)	39	1576

[1] n=2 (pen within treatment).

a,b,c Means within rows with different superscripts differ significantly ($P<0.001$).

Table 11. Allocation of a commercial ration undiluted and diluted at two levels with ground oat hulls by feed restricted broiler breeders housed in floor pens during the laying period.

Treatment	Control			D15			D30		
Age (wk)	feed (g) bird.day	SEM [1]	CP (g) bird.day	feed (g) bird.day	SEM [1]	CP (g) bird.day	feed (g) bird.day	SEM [1]	CP (g) bird.day
22.0	115.5[a]	0.4	20.3	129.5[b]	0.4	20.6	146.0[c]	0.0	21.9
23.0	115.5[a]	0.4	20.3	129.5[b]	0.4	20.6	146.0[c]	0.0	21.9
24.0	149.0[a]	0.0	26.2	166.5[b]	3.2	26.5	192.5[c]	1.1	28.9
25.0	158.0[a]	0.0	27.8	177.5	3.2	28.2	205.0[c]	0.7	30.8
26.0	177.5[a]	1.1	31.2	200.0[b]	0.7	31.8	224.0[c]	4.2	33.6
27.0	179.0[a]	0.0	31.5	200.0[b]	0.7	31.8	224.0[c]	4.2	33.6
28.0	179.0[a]	0.0	31.5	200.0[b]	0.7	31.8	224.0[c]	4.2	33.6
29.0	179.0[a]	0.0	31.5	200.0[b]	0.7	31.8	224.0[c]	4.2	33.6
30.0	184.0[a]	0.0	32.4	209.0[b]	0.0	33.2	226.0[c]	5.7	33.9
31.0	184.0[a]	0.0	32.4	209.0[b]	0.0	33.2	226.0[c]	5.7	33.9
32.0	184.0[a]	0.0	32.4	209.0[b]	0.0	33.2	226.0[c]	5.7	33.9
33.0	184.0[a]	0.0	32.4	209.0[b]	0.0	33.2	226.0[c]	5.7	33.9
34.0	179.5[a]	0.4	31.6	194.0[b]	3.5	30.8	230.0[c]	0.0	34.5
35.0	179.5[a]	0.4	31.6	194.0[b]	3.5	30.8	230.0[c]	0.0	34.5
[illegible]6.0	178.0[a]	0.7	31.3	188.0[a]	0.7	29.9	220.5[b]	3.2	33.1
37.0	178.0[a]	0.7	31.3	188.0[a]	0.7	29.9	220.5[b]	3.2	33.1
38.0	176.0[a]	0.7	31.0	195.0[b]	1.4	31.0	223.0[c]	1.4	33.5
39.0	176.0[a]	0.7	31.0	195.0[b]	1.4	31.0	223.0[c]	1.4	33.5
40.0	176.0[a]	0.7	31.0	185.0[a]	3.5	29.4	215.5[b]	3.9	32.3
41.0	176.0[a]	0.7	31.0	185.0[a]	3.5	29.4	215.5[b]	3.9	32.3
42.0	166.0[a]	2.8	29.2	184.0[b]	2.8	29.3	210.0[c]	1.4	31.5
43.0	166.0[a]	2.8	29.2	184.0[b]	2.8	29.3	210.0[c]	1.4	31.5
44.0	151.5[a]	1.1	26.7	163.0[b]	0.7	25.9	187.0[c]	1.4	28.1
45.0	151.5[a]	1.1	26.7	163.0[b]	0.7	25.9	187.0[c]	1.4	28.1
46.0	151.5[a]	1.1	26.7	163.0[b]	0.7	25.9	187.0[c]	1.4	28.1
47.0	151.0[a]	1.4	26.6	169.0[b]	1.4	26.9	188.0[c]	2.1	28.2
48.0	151.0[a]	1.4	26.6	169.0[b]	1.4	26.9	188.0[c]	2.1	28.2
49.0	151.0[a]	1.4	26.6	169.0[b]	1.4	26.9	188.0[c]	2.1	28.2
Laying Total (g/bird) (% of Control)	32529[a] (100)	120	5725	35889[b] (110.3)	9	5706	40688[c] (125.1)	340	6103

[1] n=2 (pen within treatment).

a,b,c Means within rows with different superscripts differ significantly (P<0.001).

Table 12. Feed allocation during the laying period of a commercial diet undiluted and diluted at two levels with ground oat hulls for feed restricted broiler breeder females in cages.

Treatment	Control		D15		D30	
Age (wk)	feed (g) bird.day	CP (g) bird.day	feed (g) bird.day	CP (g) bird.day	feed (g) bird.day	CP (g) bird.day
22	109.5	19.3	123.0	19.6	137.0	20.6
24	130.5	23.0	143.0	22.7	164.0	24.6
25	158.5	27.9	173.5	27.6	199.0	29.9
26	165.5	29.1	187.5	29.8	180.5	27.1
27	165.5	29.1	187.5	29.8	199.5	29.9
28	171.0	30.1	192.0	30.5	209.0	31.4
30	167.5	29.5	190.0	30.2	202.5	30.4
32	168.0	29.6	183.5	29.2	202.5	30.4
34	165.0	29.0	177.5	28.2	199.0	29.9
36	161.5	28.4	177.5	28.2	194.5	29.2
38	157.5	27.7	173.5	27.6	194.5	29.2
40	152.5	26.8	168.0	26.7	188.5	28.3
41	148.0	26.0	163.0	25.9	183.0	27.5
42	145.5	25.6	160.5	25.5	176.0	26.4
44	140.5	24.7	155.5	24.7	175.0	26.3
45	138.0	24.3	152.5	24.2	172.0	25.8
46	135.5	23.8	149.5	23.8	162.5	24.4
48	130.0	22.9	144.5	23.0	159.5	23.9
49	125.5	22.1	139.5	22.2	154.0	23.1
50	126.0	22.2	140.0	22.3	154.0	23.1
52	127.0	22.4	139.5	22.2	148.0	22.2
54	122.0	21.5	135.5	21.5	141.5	21.2
Total (% of Control)	34765 (100)	6119	38490 (110.7)	6120	42119 (121.2)	6318

[1] Calculation of feed allotment was identical for each cage within treatment, therefore SEM is not shown.

to consume the feed was significantly different between treatments in both the rearing (P=0.002) and the laying (P<0.001) periods (table 13 and table 14). Averages were calculated for three different periods, as well as the overall average for the laying period. In the rearing period, there was a significant age effect (P<0.01) in the time required to consume the daily feed allotment, as well as an age by treatment interaction (P<0.01). The greatest differences in feed consumption times occurred early in the rearing period, while towards the end of the rearing period the treatment differences disappeared (table 13). On average, the pullets completely finished their feed within a relatively short time of feeding (48, 61, and 77 minutes for Control, D15 and D30, respectively; table 13).

During lay, feed was not completely consumed until an average of 264, 349, and 489 minutes (4.4, 5.8, and 8.2 hours) in the Control, D15 and D30 treatments, respectively (table 14). The difference in the amount of time required to consume the feed between the rearing and laying periods reflects the difference in the severity of restriction between the two periods, which changes from 30% of *ad libitum* during rearing to 70% of *ad libitum* intake during lay (Yu *et al.* 1992a). Because of these differences in feed consumption time, one may expect to see differences in indicators of well-being and performance.

Stress

Behavior

The method of observation assumed uniform distribution of birds within the pen since it was not possible for the whole pen to be recorded. Results of the behavior study should therefore be interpreted with appropriate caution. Pullets in all treatments actively engaged in feeder directed spot-pecking, indicating that the level of feed restriction was severe enough in all three treatments to induce stereotypical behavior. During rearing there were no significant treatment differences in the incidence of feeder directed spot-pecking (P=0.90), eating (P=0.33), preening (P=0.82), resting (P=0.37), or drinking behavior (P=0.66) (table 15). There was, however, a decrease in the

Table 13. Time required to consume feed during the rearing period.

Treatment	Control			D15			D30		
Age (wk)	Time (min.)	n [1]	SEM	Time (min.)	n	SEM	Time (min.)	n	SEM
4.0	210.0^{c}	2	10.6	360.0^{b}	2	0.0	435.0^{a}	2	0.0
4.5	105.0^{b}	2	21.2	225.0^{a}	2	0.0	285.0^{a}	2	0.0
5.0	90.0^{b}	2	0.0	90.0^{b}	2	0.0	145.0^{a}	2	0.0
5.5	75.0^{c}	2	0.0	105.0^{b}	2	0.0	140.0^{a}	2	0.0
6.0	90.0^{a}	2	0.0	45.0^{b}	2	0.0	90.0^{a}	2	0.0
6.5	47.5	2	5.3	47.5	2	5.3	55.0	2	0.0
7.0	60.0^{b}	2	0.0	60.0^{b}	2	0.0	85.0^{a}	2	0.0
7.5	30.0^{b}	2	0.0	30.0^{b}	2	0.0	70.0^{a}	2	0.0
8.0	35.0^{b}	2	0.0	35.0^{b}	2	0.0	65.0^{a}	2	0.0
8.5	35.0	2	0.0	35.0	2	0.0	42.5	2	5.3
9.0	35.0^{b}	2	0.0	35.0^{b}	2	0.0	55.0^{a}	2	0.0
9.5	35.0^{b}	2	0.0	35.0^{b}	2	0.0	80.0^{a}	2	0.0
10.0	25.0^{b}	2	0.0	30.0^{a}	2	0.0	25.0^{b}	2	0.0
10.5	30.0	2	0.0	30.0	2	0.0	32.5	2	1.8
11.5	40.0^{b}	2	0.0	40.0^{b}	2	0.0	45.0^{a}	2	0.0
13.0	30.0	2	0.0	30.0	2	0.0	35.0	2	3.5
13.5	20.0^{b}	2	0.0	60.0^{a}	2	0.0	60.0^{a}	2	0.0
14.0	39.5	2	3.9	50.0	2	0.0	48.0	2	4.9
14.5	49.0	2	7.8	54.0	2	0.0	53.0	2	4.9
15.0	30.0^{b}	2	0.0	30.0^{b}	2	0.0	45.0^{a}	2	0.0
15.5	32.5	2	1.8	30.0	2	0.0	30.0	2	0.0
16.0	32.5^{b}	2	1.8	40.0^{a}	2	0.7	35.0^{ab}	2	0.0
16.5	35.0	2	3.5	42.5	2	1.8	35.0	2	0.0
17.0	20.5b	2	3.2	40.0^{a}	2	0.0	32.5^{ab}	2	1.8
17.5	35.0^{b}	2	0.0	35.0^{b}	2	0.0	70.0^{a}	2	0.0
18.0	30.5	2	3.9	25.0	2	0.0	31.5	2	1.1
18.5	32.5	2	1.8	40.0	2	0.0	32.5	2	1.8
19.0	35.0	2	3.5	40.0	2	0.0	40.0	2	3.5
19.5	35.0	2	3.5	45.0	2	0.0	35.0	2	0.0
Average (4-6 wk)	114.0^{a}	2	6.4	165.0^{b}	2	0.0	219.0^{c}	2	0.0
Average (6-12 wk)	35.2^{a}	2	0.4	39.0^{b}	2	0.4	54.2^{c}	2	0.3
Average (12-20 wk)	33.9	2	2..	39.3	2	0.2	40.6	2	0.5
Average (4-20 wk)	48.3^{a}	2	1.8	60.8^{b}	2	0.3	77.0^{c}	2	0.3

[1] Pen within treatment.

a,b,c Means within rows with different superscripts are significantly different ($P<0.05$).

Table 14. Time required to consume feed during the laying period.

Treatment	Control			D15			D30		
Age (wk)	Time (min.)	n [1]	SEM	Time (min.)	n	SEM	Time (min.)	n	SEM
34	320.9^{c}	40	19.6	412.1^{b}	40	26.4	566.1^{a}	40	32.1
35	263.3^{c}	40	17.3	390.0^{b}	40	25.6	512.1^{a}	40	27.6
36	248.3^{c}	40	13.6	340.6^{b}	40	17.2	432.5^{a}	40	19.5
37	303.1^{c}	40	19.5	387.9^{b}	40	17.9	502.1^{a}	40	21.4
38	222.8^{c}	40	14.1	324.8^{b}	40	14.0	453.8^{a}	40	20.2
39	234.0^{c}	40	13.2	307.5^{b}	40	20.0	460.5^{a}	40	19.9
40	234.0^{c}	40	17.6	288.0^{b}	40	15.5	438.0^{a}	40	14.9
41	288.8^{b}	40	20.9	342.9b	40	22.6	549.1^{a}	40	23.4
Average (% of Control)	264.4^{z} (100)	40	14.2	349.2^{y} (132.1)	40	16.8	489.3^{x} (185.1)	40	18.5

[1] Cages within treatment.

a,b,c Means within rows with different superscripts are significantly different ($P<0.05$).

x,y,z Means within rows with different superscripts are significantly different ($P<0.001$).

Table 15. Relative incidence of behaviors during the rearing period of feed restricted broiler breeder females housed in floor pens fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment		Control		D15		D30	
Behavior	Age (wk)	Events	SEM [1]	Events	SEM [1]	Events	SEM [1]
Feeder spot-peck	8	76.5	7.4	91.5	8.1	59.0	21.9
	15	71.5	6.0	94.5[a]	8.8	91.0	16.3
	20	78.5	2.5	40.5[b]	17.3	59.5	6.7
Other spot-peck	8	1.5	0.4	3.5	2.5	1.0	0.7
	15	18.0	12.0	11.5	6.0	1.0	0.0
	20	15.5	10.3	5.0	3.5	4.5	3.2
Feather peck	8	6.5	2.5	4.5	2.5	5.5	3.2
	15	19.5	12.4	21.0	0.7	5.5	1.8
	20	25.0	5.7	16.5	2.5	6.5	3.9
Eat	8	5.0	2.1	1.0	0.0	4.5	2.5
	15	2.0	0.0	9.5	5.3	4.5	1.8
	20	9.5	4.6	11.5	1.1	2.0	0.7
Drink	8	14.5	6.4	11.0	2.1	14.5	1.1
	15	3.0	0.7	0.0	0.0	2.5	1.1
	20	6.5	2.5	1.5	1.1	10.0	3.5
Preen	8	17.0	4.9	15.0	4.2	13.0	4.2
	15	26.0	1.4	24.0	1.4	33.5	1.1
	20	26.5	0.4	25.0	1.4	26.5	1.8
Rest	8	12.0	0.7	2.5	1.1	8.5	0.4
	15	10.0	2.8	5.0	0.0	10.0	0.7
	20	6.5	3.9	14.5	8.8	10.0	0.7

[1] n=2 pens within treatment.

a,b Means within behavior groups differ significantly ($P<0.05$).

incidence of spot-pecking within the D15 treatment at 20 weeks of age (table 15). The lack of a treatment difference in the incidence of spot-pecking may indicate that there was no difference in pullet well-being, or that one may have existed (see H/L section), but the difference was not great enough to cause a difference in the incidence of spot-pecking. Furthermore, the development of stereotypical behaviors may be learned from neighboring birds. The pens used in this study were separated by a wire mesh through which the activities of birds in neighboring pens were readily visible. This may have influenced the development of stereotypies even in less stressed birds. However, the author believes that feed restriction stress did play a role in the development of spot-pecking behavior because full fed pullets from the same hatch housed in a pen next to the birds in this study did not develop spot-pecking behavior. The spot-pecking stereotypy observed during the rearing period may have served as a coping strategy to relieve the negative effects of hunger on pullet well-being (Savory *et al.* 1992, Kennes *et al.* 1988).

Strain differences in spot-pecking behavior have been noted previously (Savory *et al.* 1992). The strain of hens used in this experiment (SHAVER) may differ from those used in other studies in the levels of stereotypical behavior. Comparisons between strains must therefore be made with caution.

There were treatment differences in the incidence of drinking ($P<0.001$) and resting behavior ($P=0.035$) during the laying period (table 16). Birds in both the D15 and the D30 treatments visited the waterer less frequently than the Control treatment. Because the Control birds have a smaller amount of feed to consume, they may be attempting to fill up on water, and thus reduce their hunger. Resting behavior was also decreased in the D15 and D30 treatments compared to the Control. This is in contrast to that found by Hocking and associates (1993), who found that *ad libitum* fed birds spent more time resting than feed restricted birds.

Table 16. Relative incidence of behaviors during the laying period (47 wk) of feed restricted broiler breeder females housed in floor pens fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control		D15		D30		FF [2]	
Behavior	Events	SEM [1]	Events	SEM [1]	Events	SEM [1]	Events	SEM [1]
Spot-peck	38.1	9.6	29.2	6.8	54.9	11.2	5.8	1.4
Drink	86.8[y]	7.5	56.6[x]	7.0	46.1[x]	5.5	44.9	3.0
Eat	29.1	12.0	26.2	7.8	38.4	9.5	152.4	4.9
Aggression	0.3	0.1	0.3	0.1	0.3	0.1	0.5	0.21
Dust bath	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1
Resting	108.1[b]	17.6	74.3[a]	13.0	72.4[a]	13.9	82.5	16.5

1 n=30 (treatment x time).

2 Full fed sister pen. Not part of experimental design; for information only.

a,b Numbers within rows followed by different superscript are significantly different ($P<0.05$).

x,y Numbers within rows followed by different superscript are significantly different ($P<0.001$).

Still picture analysis was used during the laying period to simplify the quantification of behaviors. This medium proved to complicate the verification of several of the behaviors of interest. For example, it was difficult to determine which birds with their heads near the feeder were standing, which were about to eat and which birds were spot-pecking. All birds with their heads within "striking distance" from the feeder were counted to be spot-pecking. Spot-pecks directed at the top of the sex-separate feeders were clearly distinguishable. It was virtually impossible, however, to discern spot-pecks directed at regions near the opening of the feeder from the commencement or completion of eating behavior. Although many of the spot-pecks could be clearly determined, the reported incidence of spot-pecking for the laying period is artificially high, and does not accurately indicate the actual proportion of spot-pecking that occurred. Continuous footage would have been more effective at revealing differences in the incidence of spot-pecking as a result of nutrient dilution. As a result, analysis of spot-pecking behavior around the feeder yielded inconclusive results during the laying period. It is important to note, however, that stereotypies may be habitually performed once they are an established behavior (Kennes *et al.* 1988). Since the birds developed stereotypies during the rearing period, even with good data for the laying period, it would difficult to establish whether or not the stereotypical behavior served as a coping mechanism. Because the amount of time required for complete consumption of the feed was much longer during lay than during rearing, it is likely that broiler breeders in the laying phase of production are not dependent on the spot-pecking stereotypy as a coping strategy.

Heterophil/lymphocyte ratios

There was a significant difference in the H/L ratio between treatments at 12 weeks of age ($P=0.02$), with a significantly higher H/L ratio in the Control than in the D15 and D30 treatments. The H/L ratio of the D15 and D30 treatments was not significantly different from the full fed breeders mentioned earlier, but the H/L ratio of birds in the full fed treatment (H/L=0.189) was significantly lower than that of the Control group ($P<0.001$). Increased corticosterone levels have

been implicated as a causal factor in increasing H/L ratios (Gross and Siegel 1983), although it is possible that other factors may also affect the H/L ratio. It is reasonable to speculate, however, that hunger stress in at least some of the Control birds was sufficient to cause an increase in corticosterone levels for long enough periods of time to cause an alteration of the H/L ratio, and that nutrient dilution improved pullet well-being.

The variation in mean H/L ratios on the individual bird level reflects pen level variation in that birds in the Control treatment had a higher degree of variability in H/L ratios. The standard error of the mean of the H/L ratios was much higher in the Control treatment (SEM_{bird}=0.345) than in the D15 (SEM_{bird}=0.024) and the D30 (SEM_{bird}=0.077) treatments, indicating that some birds have a more pronounced physiological response (increased H/L ratio) to feed restriction stress than others (table 17). It can be concluded, therefore, that feed restriction does not cause a uniform physiological response in SHAVER pullets. This may be due in part to disproportionate allocation of feed, or to biological differences in the physiological response to feed restriction. If the H/L ratio were due to disproportionate feed consumption, one might expect that the H/L ratio of smaller birds (receiving less feed) may be higher than that of larger birds. Regression analysis was performed to determine the relationship between BW and the H/L ratio in the Control pullets. No relationship was found (r^2=0.003; P=0.78), indicating that the reason for the variability in the H/L response is probably due to intrinsic biological factors specific to individual birds rather than disproportionate feed consumption and satiety.

The difference in the H/L ratio was not seen at the end of the rearing period (20 wk) (table 17). This may be the result of conditioning of the pullets to the stress of feed restriction. Gross and Siegel (1986) also observed that H/L ratio did not increase as much in a subsequent feed restriction challenge compared to the primary challenge. Since the difference in feed

Table 17. Heterophil lymphocyte (H/L) ratios of feed restricted broiler breeder females fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	H/L	n [1]	SEM	H/L	n	SEM	H/L	n	SEM
12	0.846[b]	48	0.413	0.269[a]	49	0.002	0.362[a]	49	0.040
20	0.039	9	0.003	0.073	9	0.022	0.113	9	0.022
54	0.409	40	0.062	0.408	40	0.058	0.334	40	0.023

[1] Individual bird.

a,b Means within rows followed by different superscript are significantly different ($P<0.05$).

consumption time decreased toward the end of the rearing period (table 13) the level of stress was probably not significantly different. However, the time required to consume the feed in both the D15 and the D30 treatments approached that of the Control, so one might expect an increase in H/L ratios toward the end of the rearing period. However, it is most probable that the pullets were able to adapt and cope to the stress, since at 20 weeks the average H/L ratios were very low in all three treatments (table 17). Conversely, spot-pecking may have improved well-being in the Control birds and thereby reduced their H/L ratios by 20 wk.

H/L ratios were not different between the treatment groups during lay (54 wk) (table 17). There are two explanations for this. First, the level of feed restriction during the laying period was less severe than during rearing, supporting the observations of Karunajeewa (1987) and Yu *et al.* (1992a). The level of stress associated with the level of feed restriction during the laying period may not be sufficient to cause a change in the H/L ratio. Alternatively, the adaptation to feed restriction stress documented by Gross and Siegel (1986) may have occurred in response to the feed restriction stress. This type of adaptation would also explain the decreased incidence of spot-pecking in the D15 birds at the end of the rearing period.

At peak egg production (35 wk) blood was collected from 20 birds of the same hatch (mentioned earlier) all of which were housed identically to the caged birds. There was no difference (P=0.95) in the H/L ratio between birds that were fed identically to the Control birds (H/L=0.190, n=10), and their full fed sisters (H/L=0.194, n=10), indicating that at peak production the level of feed restriction in the Control group is not sufficient to cause an increase in the H/L ratio.

The H/L ratio varied considerably with time (table 17). Savory (1989) reported low H/L ratios, similar to those measured in week 20, while the H/L ratios at 12 and 54 weeks are similar to those

reported by Gross and Siegel (1983, 1986). It is possible that the H/L ratio may be affected by the onset of puberty, although the reason for the differences is unclear.

Neither behavior nor the H/L ratio is a direct measure of the well-being of the hens, however, these parameters are affected in cases where well-being is almost certainly affected (Gross and Siegel 1983, Savory 1989). Although the results of the behavioral and physiological tests do not show drastic differences in stress levels, the results are not inconsistent with the hypothesis that diet dilution may improve the well-being of feed restricted broiler breeders. Two conclusions may be drawn. First, it is possible that the well-being of feed-restricted broiler breeder females is not severely affected by feed restriction, therefore no large improvements were seen as a result of nutrient dilution. However, based on the observations of the full fed birds which were not part of this study, but which coexisted in the same facility, a more conservative and probably more accurate conclusion is that nutrient dilution did not improve well-being as substantially as full feeding would. Nutrient intake may play as much of a role in satiety as volume. If this is the case further dilution with any non-nutritive substance would not improve broiler breeder well-being. This data from this study, however, are not sufficient to draw such a conclusion.

Productivity

Flock uniformity

One of the hypotheses of this experiment was that flock uniformity would increase because the time of access to the feed was increased by diet dilution. Competition for limited resources likely results in the unequal distribution of feed among the flock (Petie et al. 1982, Bennet and Leeson 1989, Karunajeewa 1987). Overweight (more aggressive or faster eating) birds can translate into a significant economic loss. Conversely, underweight (less aggressive or slower eating) birds that are allotted too much feed for their BW may also have reduced reproductive performance. Previous studies with qualitative feed restriction have focused on the limiting of single nutrients, such as individual amino acids or fatty acids. Due to variation among individual birds in the

efficiency of utilization of these nutrients, the growth of some birds was severely impaired, while that of other birds was virtually unaffected (Leeson and Summers 1991). This resulted in seriously compromised flock uniformity as low as 30-40% (of birds ±15% of mean BW). Flock uniformity is therefore a serious consideration when implementing a qualitative feed restriction regime. For restriction with one nutrient to have consistent results, a single nutrient must be found that is metabolized identically by all birds. Until such a nutrient is found, it is important that all nutrients to be restricted to the same degree. Diet dilution with a non-nutritive bulk restricts nutrients evenly may actually reduce flock uniformity problems and thereby result in an improvement in egg production may have economic advantages.

Flock uniformity in the floor pens for both the rearing and laying periods calculated as the percentage of the flock within 15% of the mean BW is presented in table 18. Flock uniformity in the caged birds is presented in table 19. There were no significant differences in flock uniformity at the 0.05 level of probability at any point during the study. Similarly, the CV was calculated for the body weights of all the birds in the study (table 20 - table 22). The trends in body weight variation are shown for those birds caged during the laying period (figure 4) and those in floor pens (figure 5). In all treatments and in both housing situations there was a substantial decrease in variation in BW at photostimulation. Since body size is an important factor in the onset of sexual maturity (Fattori *et al.* 1991), it is likely that the larger birds are quicker to partition their dietary nutrients toward reproduction. Photostimulation also marks the point in time where competition decreases for all the birds. Half of the birds were removed from the floor pens, freeing up a substantial amount of feeder space, and the other half were moved to cages, where competition was limited to a single cage mate. Further along in the reproductive cycle, as reproductive efficiency dropped, flock uniformity tended to decrease in all treatments (table 22). The lower rate of decrease in flock uniformity in the D15 and D30 treatments where feed was available for a

Table 18. Flock uniformity during the rearing and laying periods of feed restricted broiler breeder females housed in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	FU15 [1]	n [2]	SEM	FU15 [1]	n	SEM	FU15 [1]	n	SEM
0	91.98	2	1.31	93.26	2	0.40	90.80	2	0.39
2	68.13	2	4.86	71.93	2	0.48	72.55	2	0.04
4	72.07	2	7.65	72.22	2	2.64	76.24	2	3.54
8	66.01	2	7.29	70.75	2	5.47	73.24	2	0.52
12	61.12	2	4.23	71.43	2	4.98	67.08	2	0.29
16	65.40	2	4.92	66.16	2	5.13	70.28	2	1.57
20	71.91	2	1.26	69.38	2	6.44	70.97	2	1.08
26	84.54	2	0.01	87.33	2	0.02	80.60	2	0.02
34	84.54	2	0.01	84.16	2	0.02	83.57	2	0.02
47	81.72	2	0.00	82.31	2	0.03	88.14	2	0.01

1 Flock uniformity expressed as percentage of birds within ±15% of mean body weight.
2 Pen within treatment.

Table 19. Flock uniformity during the laying period [1] of feed restricted broiler breeder females housed in cages and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls (±15% method).

Treatment	Control			D15			[illegible]		
Age (wk)	FU15 [2]	n [3]	SEM	FU15 [1]	n	SEM	[illegible]		SEM
22	83.49	4	6.51	63.09	4	4.98	[illegible]	4	5.10
36	84.93	4	4.64	84.87	4	4.64	88.22	4	2.84
56	67.17	4	2.58	74.74	4	3.88	84.19	4	1.88

1 Flocks in the laying period consisted of groups of 10 cages (20 birds).
2 Flock uniformity expressed as percentage of birds within 15% of mean body weight.
3 Flock within treatment.

Table 20. Body weight variation of feed restricted broiler breeder females reared in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	CV [1]	n [2]	SEM	CV [1]	n	SEM	CV [1]	n	SEM
0	8.29	2	0.37	8.17	2	0.17	8.15	2	0.21
2	20.05	2	0.04	21.65	2	1.12	18.77	2	3.20
4	14.98	2	2.12	14.10	2	0.92	14.06	2	0.76
8	16.16	2	1.41	16.17	2	2.30	13.82	2	0.14
12	16.51	2	1.14	14.97	2	1.35	14.58	2	0.42
16	16.64	2	1.93	15.55	2	1.30	14.37	2	0.83
20	13.55	2	0.83	14.86	2	0.90	14.09	2	0.76
22	14.44	2	1.87	14.29	2	0.67	14.11	2	0.52

1 Degree of flock variation expressed as the coefficient of variation.

2 Pen within treatment.

Table 21. Body weight variation of feed restricted broiler breeder females housed in floor pens during the laying period [1] and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	CV [1]	n [2]	SEM	CV [1]	n	SEM	CV [1]	n	SEM
26	11.24	2	0.77	11.35	2	1.68	11.38	2	0.51
30	10.42	2	0.42	11.88	2	0.08	10.65	2	0.02
34	10.86	2	0.21	11.56	2	0.03	10.62	2	0.04
38	9.55	2	0.30	10.26	2	0.44	11.14	2	0.15
42	10.33	2	0.53	10.26	2	0.75	11.08	2	0.37
47	10.49	2	0.34	10.16	2	0.49	12.04	2	1.16
Regression Analysis [3]									
Slope	N/A			-0.083	6	0.027	N/A		
r^2	0.04	P=0.33		0.62	P<0.05		0.12	P=0.26	

1 Degree of flock variation expressed as the coefficient of variation.

2 Pen within treatment.

3 Regression analysis of CV against time from 26 to 47 wk (egg production period).

Table 22. Body weight variation of feed restricted broiler breeder females housed in cages during the laying period [1] and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Age (wk)	CV [2]	n [3]	SEM	CV [2]	n	SEM	CV [2]	n	SEM
22	11.82	4	1.24	16.12	4	0.68	13.39	4	1.09
24	9.95	4	0.68	13.42	4	0.87	10.65	4	0.78
26	9.08	4	0.80	10.78	4	0.71	9.58	4	0.29
28	9.24	4	0.86	10.34	4	0.61	9.64	4	0.28
30	9.42	4	0.70	9.89	4	0.75	9.02	4	0.50
32	10.59	4	0.52	10.17	4	0.99	9.17	4	0.69
34	11.04	4	0.67	10.45	4	0.91	9.51	4	0.63
36	11.05	4	0.84	10.68	4	1.02	9.67	4	0.59
38	11.37	4	0.75	10.90	4	1.06	9.65	4	0.60
40	11.99	4	0.73	10.84	4	1.11	9.63	4	0.65
42	12.16	4	0.79	11.29	4	0.97	9.76	4	0.62
44	12.89	4	0.81	11.55	4	1.06	10.04	4	0.66
46	13.14	4	0.86	11.69	4	1.06	10.05	4	0.70
48	13.51	4	0.91	11.92	4	1.07	10.28	4	0.69
50	13.92	4	0.94	12.06	4	0.93	10.49	4	0.59
52	14.75	4	1.02	12.25	4	0.89	10.81	4	0.67
54	14.89	4	1.16	12.26	4	0.83	10.71	4	0.65
56	14.79	4	0.97	12.69	4	0.86	11.19	4	0.69
Regression Analysis [4]									
Slope	0.206[a]	16	0.007	0.084[b]	16	0.008	0.058[c]	16	0.007
r^2	0.984	P<0.05		0.881	P<0.05		0.808	P<0.05	

1 Flocks in the laying period consisted of groups of 10 cages (20 birds).
2 Degree of flock variation expressed as the coefficient of variation.
3 Flock within treatment.
4 Regression analysis of CV against time from 26 to 56 wk (egg production period).
a,b Numbers within rows with different superscripts are significantly different (P<0.05).

Figure 4. Variability in body weights over the course of the study as represented by the coefficient of variation (CV). Floor pens 0-20 wk; caged birds only 22-56 wk.

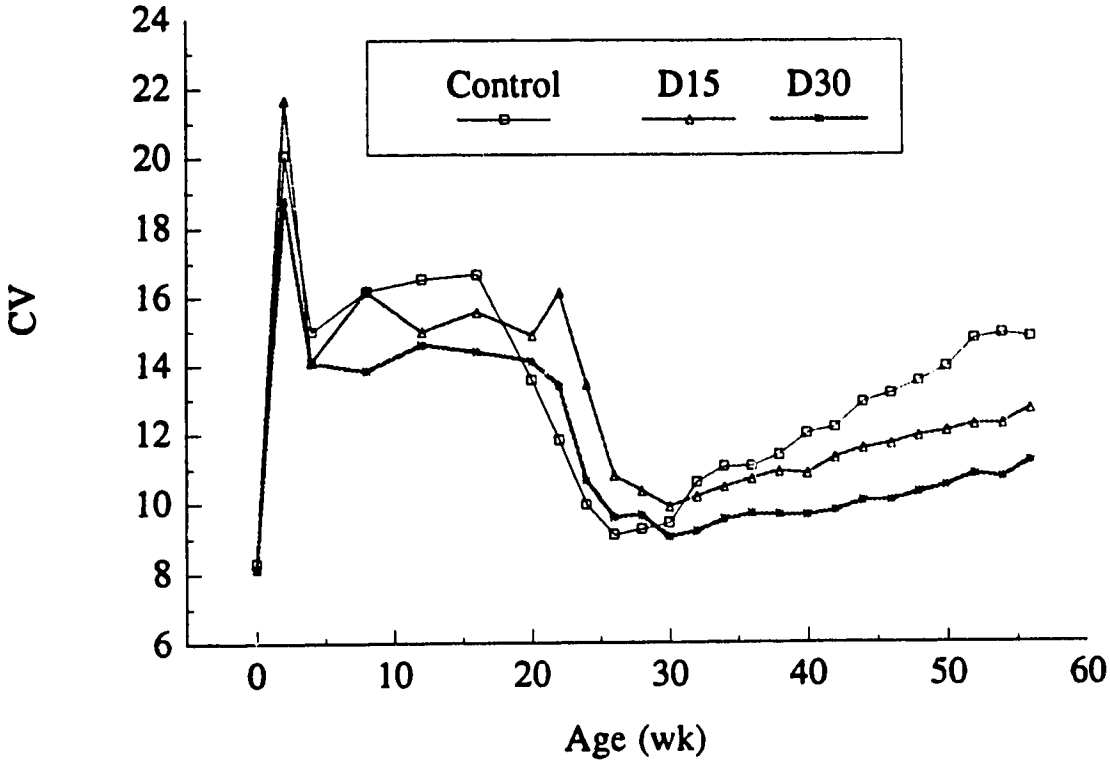
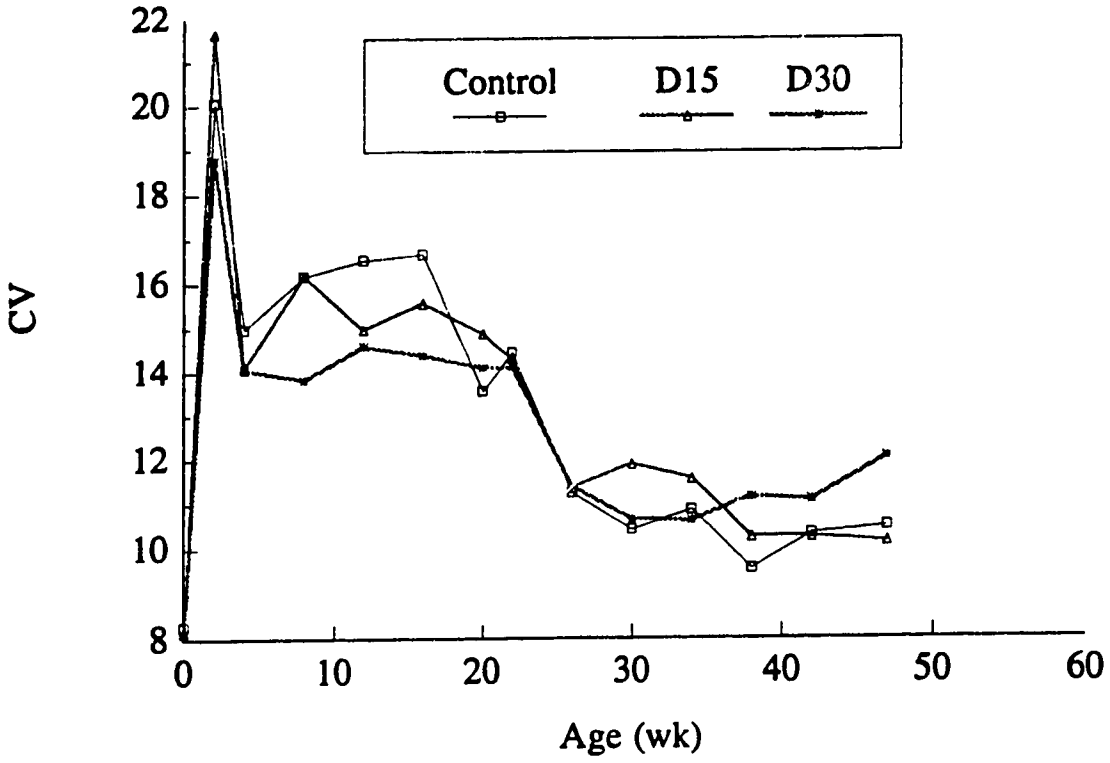


Figure 5. Variability in body weights over the course of the study as represented by the coefficient of variation (CV). Floor pens 0-56 wk.



longer portion of the day (table 14) suggests that decreased competition for feed may improve flock uniformity.

There was a significant difference in the slopes of the regression lines for each treatment (table 22). The rate of increasing variability was considerably higher in the Control ration than in the D15 and D30 rations. The slope of the line for the D30 treatment was the lowest, indicating that with higher levels of nutrient dilution, more benefits in flock uniformity will result. The results from the floor pens were not consistent with those from the caged birds. The reason for this may be that there is more severe competition for feed in the floor pens. The levels of dilution used in this study were not sufficient to cause an improvement in flock uniformity in floor pens. Because the CV and the traditional method of calculating flock uniformity are inversely related, similar conclusions were drawn with both methods. Although flock uniformity improved with diet dilution in the floor and the caged environments, a higher level of nutrient dilution is most likely required in floor pens than in cages to realize improved flock uniformity.

Feed efficiency

During the rearing period feed and CP efficiency were calculated as the amount of feed or CP, respectively, required per unit gain in BW. As expected, there was a significant increase ($P<0.001$) in the amount of feed required during the rearing period to reach the target body weights at 22 weeks when ground oat hulls were added to the diet (table 23). CP conversion was expected to be the same in all the treatments, but dilution with oat hulls resulted in more efficient utilization of the CP (table 23). Since feed consumption in the D15 and D30 treatments was less than expected (table 10), there was effectively a slight restriction of vitamins and minerals. This indicates that the nutritional value of the oat hulls as analyzed was underestimated by the feed analysis. The ME contribution of oat hulls is probably greater than the CP contribution.

Table 23. Feed conversion efficiency of feed restricted broiler breeder females fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
	FCE	n [1]	SEM	FCE	n	SEM	FCE	n	SEM
Rearing (feed/gain)	4.42^{x}	2	0.00	4.89^{y}	2	0.03	5.46^{z}	2	0.02
(% of Control)	(100.0)			(110.8)			(123.5)		
expected	*100*			*115*			*130*		
Rearing (CP/gain)	0.732^{x}	2	0.000	0.711^{y}	2	0 004	0.687^{z}	2	0.003
(% of Control)	(100.0)			(97.1)			(93.9)		
expected	*100*			*100*			*100*		
Floor pens:									
Laying (g feed/egg)	271.9^{a}	2	8.7	289.1^{a}	2	6.6	337.5^{b}	2	6.5
(% of Control)	(100.0)			(106.3)			(124.1)		
expected	*100*			*115*			*130*		
Floor pens:									
Laying (g CP/egg)	44.9	2	1.0	43.5	2	0.3	46.2	2	0.5
(% of Control)	(100.0)			(96.9)			(102.9)		
expected	*100*			*100*			*100*		
Cages:									
Laying (g feed/egg)	237.5^{x}	78	5.0	237.7^{x}	7	3.1	281.8^{y}	72	5.3
(% of Control)	(100.0)			(100.1)	6		(118.7)		
expected	*100*			*115*			*130*		
Cages:									
Laying (g CP/egg)	41.8^{x}	78	1.0	37.8^{y}	7	0.5	42.2^{x}	72	0.8
(% of Control)	(100.0)			(90.4)	6		(101.0)		
expected	*100*			*100*			*100*		

[1] Floor pens n=pen within treatment; Cages n=bird within treatment.

a,b Means within rows with different superscripts are significantly different ($P<0.05$).

x,y,z Means within rows with different superscripts are significantly different ($P<0.01$).

Feed and CP efficiency during the laying period were expressed as grams of feed and CP, respectively, required to produce a single egg. Hens in the D15 and D30 treatments were expected to consume 15% and 30% more feed, respectively than the Control birds per egg, but the same amount of CP. Feed efficiency was not significantly different than expected at the P=0.05 level of probability (χ^2 analysis) for all treatments. Feed efficiency tended to follow the egg production curve (figure 6) inversely, feed efficiency was lower during periods of low egg productivity, and higher during periods of peak egg production (table 24). Floor D15 and D30 birds used 6.3% and 24.1% more feed, respectively, than the Control birds to produce a single egg. CP efficiency was similar in all three treatments, however the D15 treatment had the lowest CP efficiency (97% of control) (table 23). In the caged birds these trends were more significant. Feed efficiency was not different in the Control and the D15 treatments, although differences were expected. CP efficiency was significantly better (P<0.001) in the D15 treatment than in either the Control treatment or the D30 treatment (table 23). Since feed consumption in the D30 treatment did not increase in proportion to the level of dilution, there was effectively a restriction in vitamin and mineral intake, and possibly in ME as well. This may account for the difference in CP efficiency between the D15 and the D30 treatments. The improvement in CP efficiency in the D15 treatment over the control may be due to improved well-being or improvements in timing of nutrient availability, since the digestive tract probably contained feed for a greater portion of the day in the D15 treatment than the Control, since the feed took longer to consume with the addition of oat hulls.

Egg production

Qualitative feed restriction was expected to cause a reduction in the level of stress in the D15 and D30 treatments, and as a result egg production was expected to increase in these treatments. The egg production curve is shown in figure 6. In the cages, the highest level of egg production occurred in the D15 treatment (P=0.01), with the moderate addition of non-nutritive bulk (table 25). The superior egg production began early in the laying cycle and persisted to 56 wk of

Figure 6. Egg production curves of broiler breeder females fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

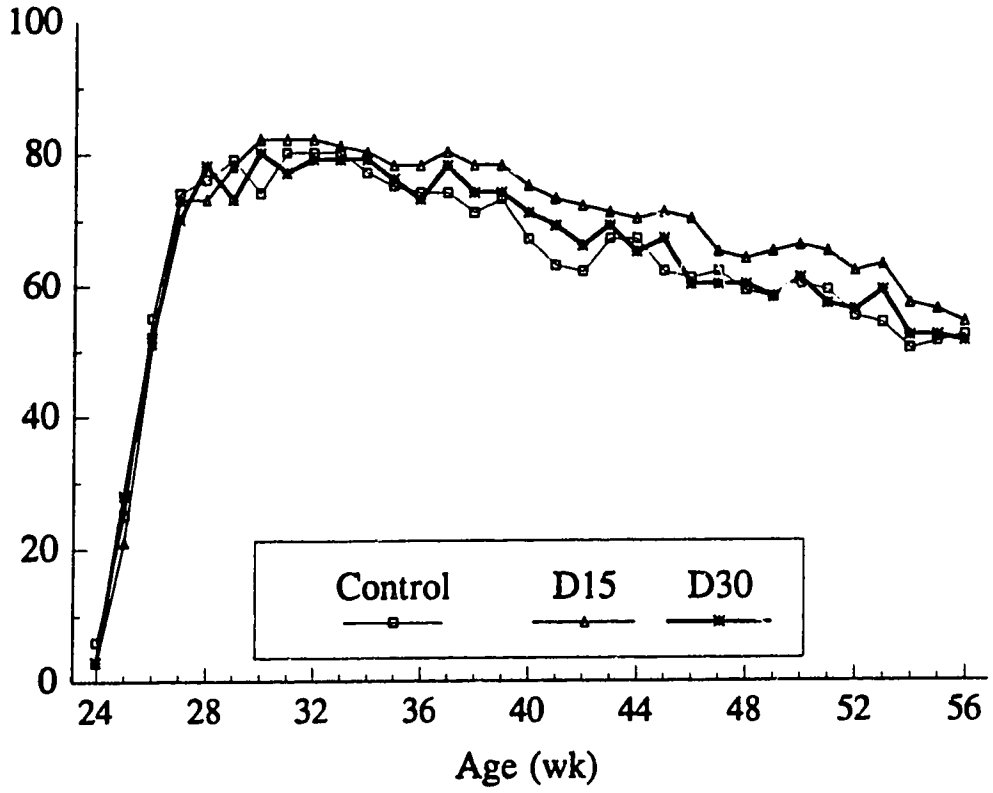


Table 24. Weekly laying period feed conversion efficiency of feed restricted broiler breeder females housed in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control		D15		D30	
Age(wk)	FCE [1]	SEM [2]	FCE [1]	SEM	FCE [1]	SEM
24	401.3	12.8	395.8	5.4	593.8	35.8
25	306.4	22.5	311.5	27.7	387.3	9.9
26	206.7	4.4	218.1	8.0	253.2	11.7
27	219.5	5.5	241.2	7.1	265.6	4.9
28	208.8	2.0	230.2	2.1	261.5	5.8
29	211.8	4.1	224.0	5.0	253.0	0.6
30	225.5	3.3	253.7	4.7	263.2	0.8
31	244.9	3.3	269.6	4.9	286.2	13.1
32	231.8	6.3	263.7	0.8	269.7	3.3
33	234.9	6.4	263.9	0.3	269.6	5.3
34	245.9	0.4	243.7	7.6	303.0	0.1
35	250.1	3.4	253.9	9.5	283.4	9.6
36	245.8	2.4	235.7	0.9	288.1	8.4
37	244.1	3.7	253.8	0.0	281.4	2.1
38	240.4	0.3	269.7	7.5	306.4	8.3
39	241.7	1.5	272.2	4.6	288.7	2.9
40	255.6	4.5	258.6	0.2	297.6	7.0
41	243.8	2.8	245.8	10.2	281.7	16.9
42	232.8	12.3	267.7	3.2	287.5	0.0
43	241.8	14.3	268.1	11.4	306.6	0.1
44	218.8	3.6	234.1	1.7	266.9	1.6
45	214.6	7.5	234.7	3.9	256.6	14.5
46	245.3	12.6	248.4	2.5	302.8	12.4
47	258.3	12.1	282.2	0.3	310.0	9.7
48	263.7	11.1	276.7	1.9	310.6	4.6
49	268.7	23.4	301.5	6.7	336.9	32.1
Average	271.9[x]		289.1[x]		337.5[y]	

1 Feed conversion efficiency (g feed/egg).

2 n=2 (pen within treatment).

x,y Means within rows with different superscripts are significantly different ($P<0.05$).

Table 25. Egg production characteristics to 56 wk of age of feed restricted broiler breeder females housed in cages and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
		n [1]	SEM		n	SEM		n	SEM
First Ovulation (d)	164.28	39	0.83	165.51	37	0.86	164.28	36	0.68
Total Eggs/bird	150.74^{y}	39	3.79	163.64^{z}	37	2.67	152.32^{y}	36	3.10
HDP [2]	0.638^{y}	39	0.004	0.689^{z}	37	0.004	0.644^{y}	36	0.004
Soft Shelled Eggs	1.65	39	0.30	3.09	37	0.71	2.39	36	0.59
Shelless Eggs	0.27^{b}	39	0.06	0.43^{ab}	37	0.09	0.64^{a}	36	0.15
Broken Shells	0.50	39	0.09	0.74	37	0.14	0.69	36	0.15
Misshapen Shells	0.05	39	0.03	0.08	37	0.04	0.06	36	0.03
Double Yolked Eggs	1.37	39	0.24	2.18	37	0.32	1.63	36	0.23
Pecked Shells	0.24	39	0.07	0.27	37	0.06	0.32	36	0.07
Multiple Ovulation Days	1.81^{a}	39	0.24	2.97^{b}	37	0.39	1.93^{a}	36	0.21
Egg weight (g)	62.28	1240	0.57	62.60	1240	0.23	63.47	1240	0.30

1 Cage within treatment.

2 Hen-day production based on 225 production days from average onset of lay to end of study. Eggs culled for poor shell are excluded.

a,b Numbers within rows with different superscripts are significantly different ($P<0.05$).

y,z Numbers within rows with different superscripts are significantly different ($P<0.01$).

age when the experiment was terminated. In the floor pens, egg production was numerically higher in both the D15 and D30 treatments than the Control (table 26), but not significantly at the 0.05 level. Onset of lay was not significantly different between the treatments (table 25). This was expected since the mean BW in all treatments was not different. Leeson and Summers (1991) indicate that individual dietary factors such as protein, energy, and linoleic acid levels may affect egg size. Given that the CP intake per egg produced was lowest in the D15 treatment (table 23), one might expect a difference in egg size. This was not the case, however. Egg weights were not significantly different between treatments (table 25).

The production of abnormal eggs may indicate that the level of feed restriction is not sufficient for optimum ovarian performance. There is evidence that the control of ovary function may be compromised in broiler breeder hens fed excess protein and energy. For example, the timing of the open period for LH release is limited to a relatively brief period of time, and this timing determines the time which ovulation (and therefore oviposition) occurs (Sharp 1989). In full-fed broiler breeders the incidence of erratic laying (eggs laid outside of the normal range of time for oviposition) has been observed to increase (Yu et al. 1992b), indicating that ovary control has been affected. Although not determined in this study there is some indirect evidence of erratic laying. Double yolked eggs are indicative of excess ovulations. Because in the case of double yolked eggs two follicles are released simultaneously and incorporated into a single shell, two mature F1 follicles could theoretically respond to the preovulatory surge of LH levels, thus indicating excessive follicle recruitment rather than loss of control of the open period. The incidence of days in which both multiple ovulations (P=0.006) and double yolked eggs (P=0.03) occurred was higher in the D15 treatment than in the Control treatment. This may indicate that the level of nutrient availability in the D15 treatment was somehow higher than in the Control. This may be the result of increased efficiency of utilization of the available nutrients in the D15 treatment. Based on the observations that feed conversion efficiency was greater in the D15 treatment and that excess

Table 26. Total egg production to 48 wk of age of feed restricted broiler breeder females housed in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls. Floor eggs and eggs with poor shells excluded.

Treatment	Control			D15			D30		
	Production	n [1]	SEM	Production	n	SEM	Production	n	SEM
Eggs/bird	127.56	2	2.27	131.13	2	0.88	132.20	2	0.30
HDP [2]	0.660	2	0.009	0.680	2	0.009	0.684	2	0.009

1 Pen within treatment.

2 Hen-day production based on 193 production days.

dietary energy is quickly allocated to the developing hierarchy of follicles (Robinson *et al.* 1993b), it is possible to conclude that the incidence of double yolked eggs indicates that the ovary was the target for excess nutrient allocation in the D15 treatment. The body weights of the birds in the D15 treatment did not at any point exceed that of the other treatments (table 8), suggesting that simultaneous follicle development and clearance may have been the preferred mode of energy partitioning.

When multiple ovipositions occur, egg shell quality may be adversely affected, since the time in which calcium can be deposited around the egg is divided between two or more eggs. Although not significantly different (P=0.076), the incidence of soft shelled eggs (eggs with shells which are not completely calcified) was numerically higher in the D15 treatment than in the Control treatment. This is probably due to the increase in multiple ovulations, which may in turn indicate excess energy intake. Although these abnormalities are of concern, the total hen-day production of the D15 treatment was superior to that of the Control and D30 treatments, and are therefore not of serious economic concern. These abnormalities may occur as some function of total egg production (1-2%), and may not be of serious concern when they occur at the levels observed in this study.

Fiber has anti-nutritive effects in chickens. Field bean hulls, for instance, depress protein and starch digestion by adsorbing digestive enzymes and thus inhibiting the action of the enzymes (Longstaff *et al.* 1991, Longstaff and McNab 1991). Reductions in digestibility are observable with cellulose alone, but much more pronounced when condensed tannins are present in the hulls (Longstaff and McNab 1991). The type of fiber used for nutrient dilution may therefore affect shell quality, and must be carefully considered when implementing programs of qualitative feed restriction.

It is possible that higher levels of nutrient dilution with fiber result in more serious anti-nutritive effects. In this experiment, significantly more membranous (shelless) eggs were produced per bird (P=0.02) in the D30 treatment than in the Control, with a median occurrence in the D15 treatment (table 25). This may be due to a higher degree of calcium adsorption by the fiber (and fiber-associated compounds) with higher levels of fiber addition to the diet, thus causing insufficient calcium availability more frequently in the D30 treatment than the Control. Creative solutions may be found to remedy these types of problems. For example, a source of calcium such as oyster shells can be provided for the hens to consume on a choice basis. Although the efficiency of calcium utilization may not be optimal, hens receiving high levels of fiber would have ample access to calcium for shell formation especially during periods of high calcium demand.

Table 27 illustrates egg production as a function of BW and flock uniformity, two important aspects of broiler breeder flock management. The effect of BW on egg production is the primary factor affecting productivity. In this study there was a difference of 40 eggs per hen between birds in the heaviest third of the BW range over the 35 week production period. The effect of flock uniformity in this experiment on egg production was secondary to the effect of body weight. Flock uniformity had very little effect on egg production.

Fertility and hatchability

Overall fertility and hatchability were not different between treatments in caged birds and floor pens (table 28 - table 31), however in the period shortly after peak production fertility and hatchability were higher in the moderate dilution (D15) treatment. This may be a function of improved well-being. Since all eggs were incubated for 21 days, very early embryonic mortality was indistinguishable from infertility. It is possible that birds in the D30 treatment are nutrient deficient because of enzyme adsorption by fiber, slower nutrient mobilization from the gut, or because of reduced nutrient intake as a result of reduced feed intake compared to expected intake

Table 27. The effect of body weight and flock uniformity differences at 56 weeks of age on egg production in feed restricted broiler breeder females fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Egg production as a function of BW and flock uniformity								
Mean Body Weight (g)	Worst Uniformity [1] (1331-1994)	n [2]	Middle Uniformity (668-1330)	n	Best Uniformity (3-667)	n	All (3-1994)	n
Heavy (3897-4362)	137.5	3	134.3	4	121.7	8	128.2	15
Medium (3431-3896)	160.9	4	152.7	23	158.3	44	156.6	71
Light (2965-3430)	-	0	168.8	12	167.8	14	168.2	26
All (2965-4362)	150.9	7	155.7	39	155.9	66	155.5	11

1 Flock uniformity based on the difference in BW(g) of the two birds in each cage. The number of birds within each cage is too small (n=2) to represent flock uniformity as the percentage of birds within ±15% of the lot mean or as the CV.

2 Individual bird.

Table 28. Fertility of feed restricted broiler breeder females housed in cages and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Period	Fertile (%)	n [1]	SEM (%)	Fertile (%)	n	SEM (%)	Fertile (%)	n	SEM (%)
Early (28-37 wk)	86.4	40	0.9	86.9	40	1.0	86.8	40	1.5
Mid (38-44 wk)	93.1[a]	40	0.8	95.9[b]	40	0.5	94.2[ab]	40	0.9
Late (45-56 wk)	89.5	40	1.4	88.6	40	1.0	88.8	40	1.2
Overall (28-56 wk)	89.0	40	0.8	89.4	40	0.7	89.1	40	1.0

1 Cage within Treatment.

a,b Means within rows with different superscripts differ significantly ($P<0.05$).

Table 29. Hatchability of feed restricted broiler breeder females housed in cages and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Period	Hatchable (%)	n [1]	SEM (%)	Hatchable (%)	n	SEM (%)	Hatchable (%)	n	SEM (%)
Early (28-37 wk)	78.3	40	1.3	78.9	40	1.4	80.3	40	1.8
Mid (38-44 wk)	85.8[a]	40	1.2	90.0[b]	40	1.1	87.9[ab]	40	1.3
Late (45-56 wk)	79.4	40	1.7	81.0	40	1.4	82.3	40	1.6
Overall (28-56 wk)	80.3	40	1.1	82.0	40	1.1	82.6	40	1.3

[1] Cage within treatment.

a,b Means within rows with different superscripts differ significantly ($P<0.07$).

Table 30. Fertility of feed restricted broiler breeder females housed in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30			Full Fed [1]		
Period	Fertile (%)	n [2]	SEM (%)	Fertile (%)	n	SEM (%)	Fertile (%)	n	SEM (%)	Fertile (%)	n	SEM (%)
Early (28-37 wk)	94.4	2	0.6	93.6	2	0.4	92.4	2	0.3	61.7	1	N/A
Mid (38-44 wk)	95.8	2	0.9	95.9	2	0.2	93.1	2	0 6	41.6	1	N/A
Late (45-47 wk)	94.4	2	1.2	93.5	2	0.1	92.5	2	0.1	41.3	1	N/A
Overall (28-47 wk)	94.8[b]	2	0.2	94.3[b]	2	0.1	92.6[a]	2	0.0	53.4	1	N/A

1 For comparison only.

2 Pen within treatment.

a,b Means within rows with different superscripts differ significantly ($P<0.05$).

Table 31. Hatchability of feed restricted broiler breeder females housed in floor pens and fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30			Full Fed [1]		
Period	Hatch (%)	n [2]	SEM (%)	Hatch (%)	n	SEM (%)	Hatch (%)	n	SEM (%)	Hatch (%)	n	SEM (%)
Early (28-37 wk)	89.0	2	0.9	86.2	2	0.6	85.0	2	0.2	53.2	1	N/A
Mid (38-44 wk)	88.8	2	1.9	87.3	2	0.9	83.9	2	0.3	35.1	1	N/A
Late (45-47 wk)	87.3	2	0.7	84.6	2	0.8	83.1	2	1.4	35.9	1	N/A
Overall (28-47 wk)	88.7^{b}	2	0.1	86.3^{ab}	2	0.7	84.4^{a}	2	0.2	45.8	1	N/A

1 For comparison only.

2 Pen within treatment.

a,b means within rows with different superscripts differ significantly ($P<0.05$).

(table 12). If nutrient deficiencies occur during the period of the day in which albumen is deposited, albumen quality may be adversely affected, thus affecting early embryonic development. Dilution of diets with cellulose may have an effect on lipid metabolism in the liver, and this may affect the quality of egg yolk and subsequent fertility or hatchability. For instance, McKay (1980) found that liver size was significantly reduced in pullets fed higher levels of fiber than those used in this experiment. The decrease in liver size may indicate that the ability of the hen to metabolize lipids was adversely affected, possibly as a result of the anti-nutritive effects of high fiber diets (Longstaff *et al.* 1991, Longstaff and McNab 1991). If the anti-nutritive effect of fiber is responsible for nutrient deficiencies leading to increased early embryonic mortality, higher levels of fiber such as those used by McKay (1980) and in this experiment (D30) would counteract any improvements in fertility and hatchability as a result of improved well-being.

Mortality

The incidence of mortality was not different between treatments during the rearing or laying periods in either the floor pens or the caged hens (table 32). The primary cause of mortality during rearing was dehydration in all treatments, and hepatic lipidosis (fatty liver) during the laying period. The distribution of cause of mortality was similar in all treatments, however the sample size was too small to perform meaningful statistics.

Further optimization

Further optimization of feeding programs for broiler breeders is undoubtedly possible. Metabolic problems related to the availability of nutrients which may be associated with qualitative feed restriction might be avoided by providing animals with choices of feedstuffs. An example of such a program may be to provide laying females with generous portions of low nutrient density rations, supplemented with tightly regulated quantities of high nutrient density feeds such as a high protein and/or energy ration early in the day to provide nutrients during the period of albumen secretion,

Table 32. Mortality in feed restricted broiler breeder females fed a commercial ration undiluted and at two levels of dilution with ground oat hulls.

Treatment	Control			D15			D30		
Period	Mortality (%)	n [1]	SEM (%)	Mortality (%)	n	SEM (%)	Mortality (%)	n	SEM (%)
Rearing (Floor) [2]	5.56	2	0.60	7.38	2	3.73	1.78	2	0.67
Laying (Floor) [3]	4.15	2	4.15	7.80	2	7.80	5.3	2	2.20
Laying (Cages) [4]	1.25	40	1.25	3.75	40	2.10	5.0	40	2.40

1 Pen or Cage within treatment.
2 0-22 weeks of age.
3 22-47 weeks of age.
4 22-56 weeks of age.

and a supply of oyster shells (calcium) late in the day or *ad libitum*. Since egg production and hatchability may be adversely affected by high protein intake (Leeson and Summers 1991), it is imperative not to overfeed protein, but to supply appropriate amounts at the right time of day. Independent control of the timing of protein and energy intake has not been studied, but high-tech strategies such as this may be effective in optimizing productivity. Implementation of feeding programs such as this, however, may be highly impractical.

Conclusions

Nutrient dilution increased the amount of time that feed was available to the birds. Although feed was available for a longer period of time in the D30 than the D15 treatment, the level of dilution in the D15 treatment was adequate to reduce the hunger stress associated with quantitative feed restriction alone. Well-being appeared to be improved in both the D15 and D30 treatments. This conclusion is based on the fact that feed was around longer in the D15 and D30 treatments, and also on the reduced H/L ratio of both the D15 and D30 treatments at 12 weeks compared to the Control. Behavioral indicators included a reduction in spot-pecking in the D15 treatment toward the end of the rearing period, and a decrease in the time spent at the drinker in both the D15 and D30 treatments during the laying period. Mortality was unaffected by nutrient dilution.

Variation in body weight was reduced in all treatments upon photostimulation. During the course of the laying period flock uniformity tended to decrease. In the caged birds the addition of oat hulls appeared to slow the gradual decrease in flock uniformity. The economic importance of this observation is unclear, since there was little indication of improved productivity as a function of flock uniformity in this experiment. Egg production was closely related to individual BW. Smaller hens produced more eggs than larger hens. When uniformity is high less birds will be affected by inappropriate feed allocations or the reproductive anomalies associated with obesity.

In the caged birds, the onset of lay was unaffected by diet dilution. The incidence of abnormal eggs was slightly higher when fiber was added to the diet. Egg production was the highest in the D15 treatment, with the same level of feed consumption per egg as the Control group. CP efficiency was the best in the D15 treatment. There was some degree of vitamin and mineral restriction, and possibly energy, in the D30 treatment, due to lower intakes of feed than expected. Furthermore, the anti-nutritive effects of high levels of fiber may have increased the effective nutrient restriction. In the floor pens a similar trend toward better egg production was observed in both the D15 and D30 treatments. Feed efficiency improvements were less clear in the floor pens than in the caged birds, possibly due to the small sample size or differences in competition between the environments. Egg weights, fertility and hatchability did not differ significantly between treatments.

The results of this study indicate that of the three levels of dilution imposed in this study, the optimal level of nutrient dilution with ground oat hulls for broiler breeders is 15% of the total feed mass. Further study is required to determine more precisely the actual optimum level of dilution for broiler breeder well-being and productivity.

Recommended changes to standard practice

Based on the results of this study, nutrient dilution appears to have merit for the broiler breeder producer. Further dilution may have additional positive effects. Instead of a simple dilution, however, the rations should be formulated to provide correct nutrient ratios. This would correct the unexpected nutrient restriction that resulted in this study from feed intakes that varied from predicted intakes. Caution must be exercised in the inclusion of additional fiber to the diet. While pure cellulose may be acceptable, other fiber-associated constituents such as tannins should be avoided because of their anti-nutritive properties. Improved well-being, higher egg production, and greater feed efficiency make nutrient dilution attractive to both producers and those concerned with animal welfare.

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Appendices

Appendix 1. University of Alberta broiler breeder rations.

Ingredient	Starter (0-3 wk)	Grower (4-14 wk)	Pre-breeder (14-20 wk)	Laying and Breeding
Ground Wheat	64.55	54.85	47.15	74.8
Stabilized Fat	-	-	-	1.0
Ground Barley	10.0	30.0	40.0	-
Soybean Meal	14.0	4.0	2.0	11.1
Corn Gluten Meal	2.0	2.0	2.0	2.0
Canola Meal	5.0	5.0	5.0	-
Ground Limestone	1.5	1.5	1.25	8.25
Biofos	1.5	1.25	1.25	1.5
Layer Premix	-	-	-	0.5
Choline Chloride Premix	0.5	0.5	0.5	0.5
Broiler Premix	0.5	0.5	0.5	-
DL Methionine	0.05	-	-	-
Iodized Salt	0.35	0.35	0.35	0.35
Amprol	0.05	0.05	-	-
Total	100.0	100.0	100.0	100.0