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STRAIN DIFFERENCES IN REPRODUCTIVE AND GROWTH TRAITS IN SINGLE COMB WHITE LEGHORN HENS (*GALLUS DOMESTICUS*)

BY

HARRY HENDRIK OOSTERHOFF

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

IN

ANIMAL SCIENCE

DEPARTMENT OF AGRICULTURAL, FOOD AND NUTRITIONAL SCIENCE

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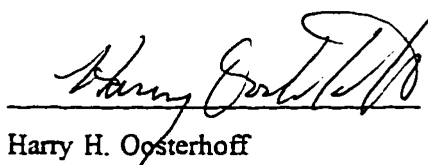

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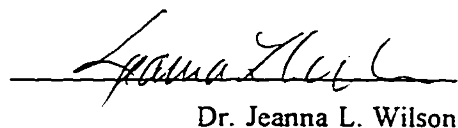

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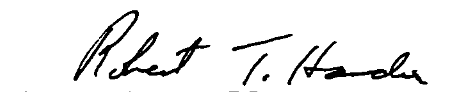

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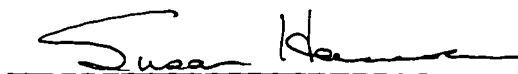

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ABSTRACT

Two experiments were conducted to examine strain differences in Single Comb White Leghorn (SCWL) chickens. In the first experiment, 300 commercial SCWL pullets of two strains differing in age at first oviposition (early maturing = EM; later maturing = LM) were reared and photostimulated at 18 wk. Select birds of each strain were killed at weekly intervals from 17 to 23 wk, at sexual maturity and at 68 wk of age for study of carcass and reproductive organ traits. Egg production was recorded for surviving hens to end of study. Carcass examination demonstrated that the EM strain allocated a greater proportion of nutrients toward reproductive function instead of growth. The LM strain hens had longer prime sequence lengths (LM, 70.2d; EM, 52.6d) as well as average sequence lengths, with similar total egg production and average egg weights.

In the second experiment, 32 commercial strain pullets (COMM) and 32 random-bred antique stock pullets (RBAS) were individually caged and photostimulated with light intensities of 1, 5, 50 or 500 lux in a 2*4 factorial design. Results indicated that RBAS birds were generally less reproductively efficient, fatter and exhibited greater variability. Decreased light intensity did not affect age of first oviposition, but increased the allocation of energy to body stores instead of reproductive organs. The incidence of internal ovulation decreased as light intensity increased.

These experiments have shown that 1) strain differences in reproductive morphology and response to photostimulation exist as a result of genetic selection in SCWL, 2) hens producing similar egg numbers may not have similar ability to produce one egg per day on a consistent basis, 3) light intensity of photostimulation has an altering effect on reproductive organ morphology and carcass traits and, 4) specific management is important to achieve the maximum production potential of each strain of SCWL.

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I. INTRODUCTION

I.1 BACKGROUND

Eggs are the product of a hen's attempt to reproduce, even if it is human knowledge that the egg is destined for the table market. A basic understanding of chicken reproductive physiology and the management strategies required to optimize reproductive performance are a prerequisite to the economical production of quality eggs for the table or hatching market. Advances in genetic selection for high egg production, large egg size, early sexual maturity, disease resistance and feed efficiency have developed modern strains of Single Comb White Leghorn (SCWL) that, compared with their ancestors, are highly efficient egg producers. Various primary breeding companies have been successful at producing different strains within the SCWL breed using a variety of breeding and selection programs. Each breeder claims distinct qualities and characteristics and these strains apparently respond differently to management practices (Anonymous, 1991; 1992; 1993). Knowledge about the differences in carcass, reproductive morphology and egg production traits between commercial strains of these highly efficient egg-type birds will better enable the industry to alter its management practices in order to increase the production of quality eggs for both the table and hatching egg markets.

I.2 ANATOMY AND PHYSIOLOGY

I.2.1 Reproductive Organ Morphology

The hen's single functional ovary is tightly attached to the left, dorsal wall of the abdominal cavity, caudal to the left lung and anterior to the left kidney (Burke, 1984). The cortex of the ovary consists of many follicles, ranging in size from tiny oocytes to a few rapidly developing yolk-filled follicles which are capable of ovulating (Gilbert, 1971). The follicles on the ovary were classified by Robinson and Etches (1986) as small white (SWF, <1 mm in diameter), large white (LWF, 2-3 mm in diameter), and small yellow (SYF, 5-10 mm in diameter). Large yellow follicles (LYF) were defined as greater than 10 mm in

diameter, although Hocking *et al.* (1987) have defined the large yolky follicles as greater than 8 mm in diameter. Below the ovarian cortex is a region rich in vascular, neural, and connective tissue called the ovarian medulla or stroma.

The ovary of an average egg-type hen contains about 12,000 tiny follicles visible under a light microscope (Burke, 1984), several thousand SWF, 10-20 LWF, 5-10 SYF, and 6-8 LYF (Gilbert, 1971; Robinson, 1986). The LYF are those which have entered the rapid growth phase and are the developing yolks for future egg production. These may be assigned to a hierarchical position according to their estimated proximity to ovulation, on the basis of size or yolk staining pattern (Yu *et al.*, 1992), with the largest LYF designated F1, the second largest F2, etc. LYF become larger as circulating lipoproteins are transferred from plasma to the ooplasm through the follicle wall (Moran, 1987). However, follicular growth does not determine a follicle's ability to ovulate (Etches *et al.*, 1983), but rather the maturation of the steroidogenic systems of the largest (F1) follicle (Johnson, 1990).

There is an optimum number of large yellow follicles required on the ovary to maintain a high rate of lay. It has been clearly shown that excess energy intake in broiler breeder hens can cause a loss of reproductive control and leads to an overabundance of follicles on the ovary. This in turn contributes to reproductive inefficiency and a condition known as erratic oviposition and defective egg syndrome (EODES), and is characterized by such problems as multiple-yolked eggs, shell deformities, internal ovulation and internal oviposition (Jaap and Muir, 1968; van Middelkoop, 1971, 1972; Hocking *et al.*, 1987, 1989; Robinson *et al.*, 1991, 1993; Yu *et al.*, 1992). However, it is also obvious that too few LYF can not support a high rate of lay (Zakaria *et al.*, 1984b); and it is generally accepted that six to eight large yellow follicles are normal for high producing egg laying strains (Gilbert, 1971; Williams and Sharp, 1978; Robinson, 1986).

The number of LYF has been shown to be influenced by age (Palmer and Bahr, 1992), feed allowance in meat-type birds (Hocking *et al.*, 1987; Yu *et al.*, 1992; Robinson *et al.*, 1993), breed and strain (Wautier, 1994). In order to maintain a consistent number of LYF,

one slow growing SWF must be recruited into the rapid growth phase each day. Zakaria *et al.* (1984a) found that a new follicle was transformed into the rapid growth phase each day between 8-14 h after the ovulation of the F1 follicle. The hierarchical system of follicular development from 1-3 mm in diameter, however, demonstrates the likelihood that recruitment must be occurring below this level (Gilbert and Wells, 1984).

Inter-sequence pauses can either be caused by the failure of a follicle to be recruited into the hierarchy of rapidly growing LYF (Williams and Sharp, 1978; Zakaria *et al.* 1984b), or by the hen's failure to ovulate. The absence of a mature follicle on the ovary may also be caused by follicular atresia (Waddington *et al.*, 1985) or some other factor such as disease which may inhibit follicular growth and development. The majority of follicles undergoing atresia will do so in the slow growing phase, and it has been suggested that this process may be one of the controlling mechanisms regulating ovulation (Gilbert *et al.*, 1983).

Failure to ovulate may be the result of the natural resetting of the circadian clock. If egg development takes longer than 24 h, the expected time of each successive ovulation becomes later each day. The expected time of ovulation will eventually occur outside the "open period for luteinizing hormone (LH) release", as described in detail in a later section. The follicle will not ovulate and this causes a skipped or pause day. Once a follicle has been recruited into the hierarchy of LYF, however, it has a high likelihood of ovulating (Gilbert *et al.*, 1983).

Each developing follicle consists of an oocyte and a surrounding perivitelline layer, whose fibrous mesh contains the mass of yolky material upon ovulation. At ovulation, a rupture occurs along the stigma which is a region of collagenous tissue lacking the connective and vascular tissue that covers the remainder of the follicle (van Krey, 1990).

I.2.2 Endocrinological Control of Reproduction

Reproduction and hypothalamo-hypophyseal-adrenal activity in chickens have been observed to follow both circadian and seasonal rhythms (Majsa and Péczely, 1976; Majsa *et*

al., 1976). The cycle of hormonal control of ovulation can be summarized in three general levels: 1) progesterone from the follicles stimulates the hypothalamus to produce gonadotropin-releasing hormone (GnRH), 2) GnRH stimulates the anterior pituitary to release luteinizing hormone (LH) and follicle stimulating hormone (FSH), 3) LH stimulates the granulosa cells of the largest follicle to produce more progesterone, which in turn positively affects the hypothalamus. In chickens, LH promotes steroidogenesis and stimulates ovulation (Etches, 1990).

The SYF are the principle source of estrogens (Robinson & Etches, 1986) in the domestic hen. At the early stages of follicular development, progestins, androgens, and estrogens are predominantly (if not solely) produced by the theca cells of small (≤ 8 mm) follicles (Tilly *et al.*, 1991). Granulosa cells apparently become steroidogenically competent and begin producing progesterone under the stimulatory regulation of FSH during the time that the follicle increases in size from 6-8 mm to 9-12 mm in diameter (Tilly *et al.*, 1991). As the follicles develop through the yolk-filled hierarchy, progesterone produced in the granulosa cells is metabolized in the theca cells to produce increasing quantities of androgens, while the production of estrogens decrease. Large yellow follicles utilize progesterone as a substrate for the increasing production of androstenedione, which reaches a maximum when the follicle occupies the F_3 position about 12-20 h prior to ovulation (Robinson and Etches, 1986). The largest follicle (F1) is said to be "competent" to ovulate when it begins secreting large quantities of progesterone. The increased follicular output of progesterone occurs when the F1 follicle loses the ability to convert progesterone to androstenedione. Ultimately, the increased progesterone production provides the necessary positive feedback loop to stimulate the release of additional GnRH. It appears that a threshold level is reached and it is generally accepted that the resultant surge in plasma LH concentrations 4 to 6 h prior to ovulation (Johnson and van Tienhoven, 1980) is required for ovulation to occur (Etches, 1996).

Estrogens produced by the SYF stimulate the formation of yolk precursors by the liver (Redshaw and Follett, 1972; van Tienhoven, 1981). They are also important for sensitizing

the hypothalamic-pituitary axis to progesterone (Wilson and Sharp, 1976), deposition of calcium in the medullary of long bones (Etches, 1987), stimulating and maintaining oviductal function, and developing the secondary sex traits (Johnson, 1986). However, estrogens are not considered to play a major role in the regulation of the ovulatory cycle (Etches, 1990).

Prostaglandins (PG) are found in the wall of the F1 follicle, but are produced in large amounts by the post-ovulatory follicle (POF) about 24 h after its own ovulation (Day and Nalbandov, 1977). The peak peripheral plasma concentration of PG has been found to coincide with time of oviposition in chickens (Hammond *et al.*, 1980; Olson and Hertelendy, 1981; Olson *et al.*, 1986; Saito *et al.*, 1987ab). It has been concluded that the PG released into the blood stream by the POF stimulate uterine (shell gland) contractions causing oviposition (Shimada *et al.*, 1983; Shimada and Saito, 1989), but PG probably does not have a regulatory role in the ovulatory cycle (Day and Nalbandov, 1977). Burke (1984) has reported that removal of the POF or its granulosa cell layer will delay oviposition of the egg which emanated from it, in some cases for days. Because PG-E is known to cause relaxation of the vaginal sphincter and PG-F is a smooth muscle stimulator, it is generally accepted as facilitating oviposition of the egg (Etches, 1996). This is supported by the works of Hargrove and Ottinger (1992) who caused premature oviposition of soft-shelled eggs by PG injections, and the findings of Hester *et al.* (1991) who found increased PG-F concentrations coincident with premature oviposition of soft-shelled and shell-less chicken eggs.

FSH produced by the anterior pituitary is believed to be responsible for follicular recruitment and growth (Mitchell, 1970; Masuda *et al.*, 1984; Palmer and Bahr, 1992). FSH has been found to stimulate granulosa cell development in small follicles and promote progesterone production by these cells in follicles between 9 to 12 mm in diameter, *in vitro* (Tilly *et al.*, 1991; Johnson, 1993). However, Robinson *et al.* (1988) concluded that FSH may play a very limited role in steroidogenesis when compared to LH.

Besides follicle maturity, a second factor known as the open period for LH release, also controls whether ovulation will occur. This system is believed to be circadian in nature

(Majsa *et al.*, 1976), and constrains the release of gonadotropins from the anterior pituitary to an approximate 8 h period each day (Robinson *et al.*, 1993). In order to be circadian, a physiological system must shift to respond to changes in the environmental light/dark cycle in an effort to remain in constant relationship (Etches *et al.*, 1984). This has been shown to occur both in studies using photoschedules which did not correspond to the solar day, and in studies utilizing ahemeral light/dark cycles. In these lighting regimes, the interval between consecutive modal times of oviposition is equal to the period of the light/dark cycle and egg laying is maintained during the photophase (Etches *et al.*, 1984).

Etches *et al.* (1984) have examined the potential role of the adrenal gland as the pacemaker regulating the timing of the pre-ovulatory surge of LH because plasma concentrations of corticosterone are known to also follow a circadian rhythm (Etches. 1979). Corticosterone has the ability to block the photoperiodic response, although its action does not alter pituitary gland functioning directly, but rather it appears to block the hypothalamic inputs to the pituitary (Etches *et al.*, 1984).

It is generally agreed that the transition from photophase to scotophase is the major environmental cue for the physiological system that entrains the timing of ovulation (Bhatti and Morris, 1978a,b). Although as little as 1.25 h of darkness appears to be sufficient, it has been shown that the percentage of ovipositions included in the modal 8 h of lay increased as scotophase length is increased from 1 to 6 h (Bhatti and Morris, 1978a). When ovulation does occur within the constraints of the open period, it normally follows the previous oviposition within 15-60 min, regardless of photoschedule (Etches, 1990).

I.2.3 Egg Formation and the Reproductive Tract

At ovulation, the follicle ruptures at the stigma, releasing the developed yolk or ovum on its journey down the oviduct. The single, functional left oviduct is a continuous tube comprised of seven layers that can be divided into five regions: infundibulum, magnum, isthmus, shell gland and vagina. The right oviduct is normally only a small nonfunctional

vestige attached to the cloaca, although under abnormal conditions it may become fluid-filled and enlarged (Somes *et al.*, 1990).

The released ovum is engulfed by the motile, funnel-shaped tissue of the infundibulum within about 20 min of ovulation. If motile sperm are present, the infundibulum acts as the site of fertilization. The infundibulum is about 9 cm long and it takes about 15 min for the ovum to pass through it. The ovum passes from the infundibulum to the largest portion of the oviduct called the magnum (33 - 50 cm in length). Albumen is secreted around the yolk by cells within the ridges of the magnum wall as it slowly rolls and twists through it for a period of about 3 h (Etches, 1996).

The 10 cm long isthmus secretes the 2 shell membranes that form the egg's enclosing sac in a process which takes about 1.5 h. These membranes hold in the egg's contents and provide a support for the shell to be deposited on. On completion of the membranes, the egg passes into the shell gland where it stays for approximately 20 h. The shell-less egg is first plumped with approximately 15 g of water, Na^+, K^+ and Cl^-, becoming egg-shaped, and the calcium carbonate shell is deposited around it. The egg is then pushed through the vagina where it is coated with bloom, a glycoprotein cuticle necessary to prevent excess moisture loss. Finally, the completed egg moves into the cloaca, turns around end for end and is pushed out of the vent, pointed end first. For a more detailed description of oviduct form and function, the reader is referred to review articles by Solomon, (1983), Johnson (1986), Proudman (1995) or Etches (1996).

I.2.4 Calcium

Egg laying in the domestic chicken represents a major challenge to the regulation of calcium metabolism. Freeman (1984) reported that the eggs of the domestic fowl contain 5 g of calcium in the shell and 26 mg of calcium in the yolk, while Etches (1987) reported that an average egg contains 2.3 g and 25 mg of calcium in the shell and yolk, respectively. In order to supply these quantities of calcium, layer diets are formulated to provide 2.8 to 4.0%

calcium and 0.35 to 0.47% available phosphorous depending on feed intake per day (Leeson and Summers, 1991). Keshavarz and Nakajima (1993) found that the NRC (National Research Council, 1984) requirement of 3.75 g of calcium per hen per day was adequate for modern high-producing commercial strains of laying hens. However, the source of calcium may play a role because oyster shell was effective in improving shell quality even when the diet contained plentiful calcium (Keshavarz and Nakajima, 1993).

The knowledge that increasing levels of androgens and estrogens lead to calcium storage in medullary bone has led to the proposal that decreasing levels of estrogen lead to calcium resorption (Simkiss, 1967). Declining levels of estrogen are thought to sensitize the medullary bone to osteoclastic activity stimulated by parathyroid hormone and 1,25 dihydroxy-vitamin D_3 (Etches, 1987). The calcification process is associated with a decline in the plasma concentration of both total and ionized calcium (Hertelendy and Taylor, 1961; Taylor and Hertelendy, 1961) and this drop may provide the stimulus for both parathyroid hormone and 1,25 dihydroxy-vitamin D_3 release, which aid in the calcification process (Soares, 1984; Etches, 1987).

Ruschkowski and Hart (1992) found that egg production and feed consumption in calcium and vitamin D-deficient hens were significantly less than control hens after 8 wk on their respective diets. Deficient birds which had ceased laying had consistently lower mean plasma estradiol-17β and progesterone concentrations, ovary and oviduct weights than laying controls. This agrees with previous results of Gilbert *et al.* (1981), who also found a decrease in food consumption and egg production as dietary calcium decreased. These authors also concluded that the primary mechanism of controlling calcium loss with diets deficient in calcium involved the regulation of the number of ovulations or eggs produced, rather than alterations in shell quality. However, the response noticed first would be a reduction in quantity of shell deposited as the time interval involved for shell deposition is within 24 h whereas yolk deposition occupies several days (7 to 10). Taylor (1965) suggested that egg production ceases with calcium deficiency as a result of decreased diffusible calcium levels in

the blood. Hypothalamic stimulation of the anterior pituitary is reduced and causes a reduction in gonadotrophin secretion. Luck and Scanes (1979) proposed that calcium deficiency caused hypothalamic insensitivity to progesterone or resulted in an insufficient storage of LH releasing hormone in the hypothalamic neurosecretory cells. In either case, the ionic concentration of plasma calcium may fall below some threshold level during egg shell calcification and reduce the secretion of gonadotrophin, effectively slowing the rate of follicular growth. As follicular development slows, there may be a reduction in the rates of estrogen secretion and yolk synthesis by the liver, and the net result may be a reduction in egg production (Taylor, 1972). Gilbert *et al.* (1981) suggested that any level of dietary calcium less than 35 g/kg, however slight it may be, would adversely affect egg production. Laying hens ceased to lay when the concentration of plasma ionised calcium decreased lower than 1.0 mM (Luck and Scanes, 1979).

In a later study, Clunies *et al.* (1992) found no effect on egg weight or egg production, with differences in shell weight when feeding diets containing between 2.5 and 4.5% calcium and 0.45% phosphorus over a 15 d period. Although this study was relatively short-term, it suggests that egg quality is compromised before calcium deficiency affects egg production. Additionally, these authors did not observe increases in feed intake on shell-forming days to compensate for the low levels of dietary calcium. Although this was in contrast to Roland *et al.* (1985) who reported an inverse relationship between dietary calcium and feed intake, it is more consistent with the findings of decreased feed intake reported by Gilbert *et al.* (1981) and Ruschkowski and Hart (1992). Clunies *et al.* (1992) concluded that calcium intake must be increased in order to increase shell quality and weight because hens were unable to fully compensate for inadequate dietary calcium by increasing feed intake or calcium retention. Instead, deficiencies in dietary calcium resulted in an apparent increase of mineral mobilization from bone, which if prolonged, causes cage layer fatique.

I.2.5 Laying Patterns

Chickens lay eggs in "sequences" or "clutches" of varying length, with one or more non-laying "pause" days between consecutive sequences. The first egg of a sequence is laid shortly after "lights on" or dawn, with each following day's egg being laid slightly later in the day. The last egg of a particular sequence is laid about 8 h after the dawn signal and no egg is laid the following day causing the sequence pause. After one or more pause days, a new sequence begins. As discussed earlier, it is both the hormonal maturity of the follicle and the open period for LH release that control ovulation, with oviposition occurring approximately 24-26 h later. Although the open period remains at the same time each day, governed by the circadian rhythm, the time of maturity of the F1 follicle seems to be slightly later each day. If the follicle becomes "competent" after the open period is over, the follicle must wait until the following day for its pre-ovulatory LH surge, and this creates the pause day (Etches, 1996).

Sequence length is closely related to production rates, and peak production occurs at the same time as the majority of hens are laying their longest or "prime" uninterrupted laying sequence. In modern SCWL, prime sequence lengths of 68.7, 81.7 and 82.4 d were recorded for hens photostimulated at 16, 18 and 20 wk of age, respectively (Robinson *et al.*, 1996). Robinson *et al.* (1990) have previously reported the correlation between the length of the prime sequence and total egg output as r=0.3992.

I.2.6 Photoperiodism

The breeding season of many animals and birds is regulated by photoperiod. Among the common domestic mammal species, the female cat, horse, sheep and goat are known to have reproduction cycles which are affected by photoperiod. Queens and mares become anestrous late in the fall due to decreasing light, while ewes and does re-establish ovarian activity with decreasing light (Stabenfeldt and Edqvist, 1984). In mammals, the eyes have been reported as an essential component of photoperiodic detection (Wurtman, 1967, 1974). Neural impulses regulate melatonin release by the pineal gland and this is believed to

influence reproductive behaviour in response to light (Reiter, 1980; Follett, 1985) In mammals, the suprachiasmatic hypothalamic nucleus appears to be a key component of the biological clock (Moore, 1983) and is also of possible importance in birds. Advis and Contijoch (1993) have suggested that the hypothalamic median eminence is probably a major site of neuroendocrine control of reproduction in hens.

Photoperiod serves as a natural timing device in seasonal breeding avian species, regulating moulting, migration, and reproductive activity. Rowan (1925) first published data on the photoperiodic effect in birds, by inducing reproductive behaviour using artificial light. Since that time, developments in our understanding of photoperiodism in domestic fowl has been well documented and the reader is referred to works by Whetham (1933), Wolfson (1966), Harrison (1972), Homma *et al.* (1980), Sharp (1993), Morris (1994), and Etches (1996).

I.2.7 Mechanism of Light Perception

The knowledge that photoreceptors in the eyes of birds are not solely responsible for reproductive control is generally accepted. Work by Menaker and Keatts (1968) and Menaker *et al.* (1970) using sparrows suggests extra-retinal light perception in birds and that the eyes are not necessary for photoperiodic photoreception. Response to changes in daily photoperiod length in enucleated and enucleated-pinealectomized Leghorn hens demonstrates the presence of a photoreceptive mechanism independent of the eye and the pineal which is capable of stimulation and retardation of gonadal function (Harrison, 1972). Therefore, the pineal gland does not seem to play an essential role in photoperiodic response either (Homma *et al.*, 1967; Siopes and Wilson, 1974; Simpson *et al.*, 1983; Johnson and van Tienhoven, 1984; John *et al.*, 1986; Siopes and Underwood, 1987). Ralph *et al.* (1975) also reported on work with blinded chickens which indicated the eye is not required for light perception and non-retinal photoreceptors must be present to produce the observed sexual response.

Homma *et al.* (1980) hypothesized a double receptor model of avian photoperiodism,

which proposes the importance of photoreceptors located in the brain near the hypothalamus as important, in addition to the eyes. These authors have previously reported that the eyes are involved in the photosexual response in Japanese quail (Homma *et al.*, 1972; Siopes and Wilson, 1974). Implantation of radioluminous beads near the hypothalamus of Japanese quail was sufficient to stimulate reproductive development (Homma *et al.*, 1980). Foster and Follett (1985) reported that light absorption through the skull and brain of Japanese quail suggests that the photoperiodic response involves a rhodopsin-like photopigment in or near the hypothalamic region. Further evidence that hypothalamic neurones are involved in the avian photoperiodic response was provided by the photoperiodic activation of nucleur *fos*-like immunoreactive proteins within the neurones of the basal tuberal hypothalamus in Japanese quail (Meddle and Follett, 1995). Although the eye is not essential for egg production, Harrison (1974) has suggested that the eye may still be involved in the photoperiodic control of oviposition time. Siopes and Wilson (1980) concluded that although extra-retinal photoreception is well established in birds, the eye should not be discounted as a photoreceptor in the photosexual process. Lu *et al.* (1995) indicate that the circadian clock regulates retinal sensitivity to light and suggest that melatonin may mediate some or all of this effect through a central site rather than a direct effect of the hormone in the eye.

Photostimulation in chickens occurs when an increase in daylength is interpreted as the signal for the onset of reproductive function. This response consists of a photoreceptor that is able to transform photon energy to neural impulses. The photoreceptor and biological clock provide these impulses to stimulate the maturation of the hypothalamic-anterior pituitary-ovarian axis by stimulating the neurons synthesizing and secreting GnRH (Sharp, 1993). The GnRH neurons have terminals in the median eminence, where GnRH is released to regulate the secretion of gonadotropins from the anterior pituitary gland (Sharp, 1993). Growth and function of the avian ovary are associated with the increased levels of these hormones which can be observed within days of photostimulation (Burke and Dennison, 1980; Dunn and Sharp, 1990; Sharp, 1993). Egg production is initiated when the first ovarian follicle matures.

I.3 PHOTOPERIOD MANAGEMENT

Photoperiod manipulation is a common and powerful management tool used in poultry production to control reproductive performance. Although a superior lighting regime is difficult to isolate, understanding the principles of a hen's response to light is useful in designing systems to satisfy specific management needs. Increasing the length of the light period is commonly used to photostimulate pullets near age of sexual maturity in order to advance age at sexual maturity, control egg size, decrease flock variability and increase the rate of lay. Decreasing photoperiod generally has the opposite effect by delaying sexual maturity and causing the production of fewer, but larger eggs (Morris, 1994).

Aside from the effect of light, the egg production of hens follows some general principles. After sexual maturity, egg production increases rapidly to a maximum of one egg per day. In flocks of layers, production will approach 100 percent of hens housed as all birds near their peak rate of production. This high flock production rate is directly influenced by the hens' sequence or clutch lengths and is reduced by pause days. If a hen has the ability to produce one egg every 24 h, she is likely to have long sequences (Fraps, 1955). SCWL have been reported to produce prime sequences up to 82.4 d in length (Robinson *et al.* 1996). Production of long sequences implies that time interval between ovipositions is very close to 24 h (Etches and Schoch, 1984; Yoo *et al.*, 1986). Egg weight and size increase from about 42 - 44 g to about 62 - 65 g between initiation of lay and 68 wk of age (Anonymous, 1991; 1992; 1993). The total time required to produce the egg also increases with the increase in egg size. This caused a lengthening of lag time (the difference in time of day that the current egg is laid relative to the previous day's egg). As each new egg is laid progressively later in the day, the likelihood increases that a follicle matures on a given day after the end of the open period for LH release. This follicle must then wait to ovulate until the following day's LH surge, causing a pause day (Etches and Schoch, 1984).

Since light manipulation is known to be effective in management of reproductive function, non-traditional lighting regimes have been proposed. At least two types of

alternative lighting regimes can be examined for this purpose. Ahemeral (non-24 h cycles) have been discussed as early as 1941, (Byerly and Moore) who suggested that hens might lay more eggs if they were kept under a light-dark cycle closely matching the time needed for the specific hen to produce one egg. During the perceived energy crisis of the 1970s and 1980s, intermittent lighting regimes were promoted to conserve energy and decrease utility costs.

I.3.1 Intermittent Lighting

Traditional lighting schedules maintain a constant photoperiod to represent day and another constant dark period to represent night. Typical examples of traditional lighting schedules are 24 h cycles for short days consisting of a light period of 8 h and a dark period of 16 h (8L:16D) or for long days of 14L:10D. Birds appear to perceive the initial light signal that follows a prolonged dark period as the signal for dawn or the beginning of the day. However, it has been found that a continuous photoperiod is not required for hens to perceive the daylight signal. On a split type of intermittent lighting regime with 3L:9D:1L:11D, hens perceive the dawn by the 3 h of light following the 11 h night. Even though the remainder of the day is in darkness for 9 h, hens still behave as if daylength were long because the photosensitive period in the evening is illuminated by the 1 h of light. This type of photoschedule has the effect of increasing feed efficiency with very little compromise to rate of egg production (Etches, 1996), likely from decreased activity. However, this type of photoschedule severely limits the time in which hens can access food and water, and this raises concerns during the high nutrient demands of peak egg production.

Intermittent schedules with alternating periods of light and dark throughout the day have also been studied. An example of such a program has a day signal consisting of 15 periods of 15 min lighting, each separated by a 45 min dark period, then followed by 9 h 45 min of constant night (14(0.25L:0.75D):0.25L:9.75D). This schedule illuminates a sufficiently large portion of the photoschedule to initiate a full photoperiodic response (Morris, 1994). A similar system developed by Ralston Purina in the USA was called the Biomittent lighting

program (16(0.25L:0.75D):8D) (Midgley *et al.*, 1988; Morris *et al.*, 1990). Although the justification for this system was to reduce electrical and utility requirements, the decrease in feed consumption probably produced greater financial savings. Switching lights off during much of the working day reduced bird activity, lowering bird energy requirements, and resulted in an approximate feed saving of 5% (Midgley *et al.*, 1988; Morris *et al.*, 1990), although this was partly offset by the need to increase dietary protein content. Lewis *et al.* (1992) also found that mortality was decreased by intermittent lighting programs.

Intermittent lighting programs have not gained wide acceptance in commercial poultry production. Although diets can become more concentrated in protein and calcium, there is still a general decline in egg size and shell quality because of the decreased consumption of feed. Additionally, strains of layers which already exhibit decreased appetite appear to have difficulty maintaining sufficient body weight for peak egg production under intermittent lighting schedules. In naturally mating breeder flocks, an increase in eggs laid on the floor is expected as the lights are turned off part of the time that hens need to find nesting boxes.

I.3.2 Ahemeral Lighting

Ahemeral lighting is defined as lighting cycles which do not conform to the 24 h solar day and they are of two general types: short (< 24 h) and long (> 24 h). Much of the work on long cycles has been provided by T.R. Morris and associates (Morris, 1973, 1978; Bhatti and Morris, 1978a; Morris and Bhatti, 1978; Shanawany, 1993; Shanawany *et al.*, 1993a,b). Short cycles have been reviewed by Marks *et al.* (1968), Cahaner and Abplanalp (1979) and Naito *et al.* (1990).

Short ahemeral cycles are of primary practical importance for identifying hens with rapid rates of follicular maturation. Since total egg production is a function of sequence length which is in turn dependent on rate of follicular maturation, selection for hens with rapid or follicular maturation rates of less than 24 h will identify those birds with the ability to produce long egg sequences (Marks *et al.*, 1968). Results of a study on selection for high egg

numbers under 22 h short day cycles resulted in genetic improvement due partially to shorter egg intervals (Cahaner and Abplanalp, 1979). Birds with rapid follicular maturation rates are characterized by their ability to produce more than one egg per 24 h when they are placed on short cycles. However, birds that have longer follicular maturation rates and short sequences on normal 24 h lighting will have even shorter sequence lengths when placed on short ahemeral days (Cahaner and Abplanalp, 1979).

Long ahemeral cycles generally have the opposite effect. Birds with the ability to produce one egg per 23-24 h will produce fewer eggs than under 24 h daylength because timing of ovulation is delayed every day as the bird "waits" for the dusk signal. However, birds with slower follicular maturation rates will exhibit increased rates of lay because of a reduction in pause days. This was demonstrated in an experiment by Shanawany *et al.* (1993a). Under 24 h cycles, birds with short (<6 eggs) sequence lengths produced an average of one egg per 34.2 h. Average rate of lay per hen was increased to an egg every 30 h under 28 h cycles due to increased sequence length. Birds with long sequences (>6 eggs) produced an average of an egg every 27 h under normal cycle length. Although their sequence length was also lengthened under the long ahemeral days, the average time between each egg was also increased to 29 h and therefore rate of lay decreased.

Associated with long ahemeral daylength is an increase in both egg size and shell quality and thickness. Long ahemeral days have been advocated as a management tool to increase egg size during the first few weeks of production, specifically in flocks photostimulated at a young age. One major drawback is the effect that large eggs have on hen welfare when they are laid early in lay. Robinson (1993) has reported that oviductal prolapse, caused primarily by large initial egg size, is an important contributing factor to early mortality in Alberta's commercial SCWL flocks. However, there is an economic advantage to producing a greater total number of large eggs. Prices paid to producers per dozen eggs in Canada vary slightly by province but the current price schedule in Alberta increases with egg size from $0.85 per dozen for small up to $1.35 for large and extra large (> 56 g) (Anonymous, 1997).

Primary breeder objectives for egg weight by commercial strains reach 56 g at approximately 28 - 31 wk, and increase throughout the laying period (Anonymous, 1991; 1992; 1993). Although long ahemeral cycles increase egg size, and could be economically beneficial prior to 28 wk of age, there is generally a negative economic return in increased production costs, especially in the U.S.A. and Canada where premiums are generally not paid for extra-large eggs. Long ahemeral days are generally proposed in the later periods of the laying year, which worsens the naturally occuring trend toward increasing egg size and decreasing shell quality.

Ahemeral lighting programs are also subject to practical difficulties. In many parts of the world, completely light-tight housing is unavailable or impractical, and therefore ahemeral lighting regimes are difficult to implement. Scheduling labour and caring for birds become difficult when the light phase does not coincide with the solar or working day. This is a general deterrent to the implementation of ahemeral lighting programs, even though alternating cycles of bright and dim light rather than light and darkness may have practical possibilities. Shanawany (1993) reported that an increased percentage of eggs laid on the floor is a problem repeatedly encountered when long light-dark cycles are used. This may be due to the increased incidence of eggs which are apparently laid in the dark under long ahemeral cycles (Biellier and Ostmann, 1960; Morris, 1973; Etches *et al*; 1984; Etches, 1996).

I.3.3 Effective Photoperiod

Effective photoperiod (P) has been defined as the actual duration of the illuminated period (p) plus the difference between the ahemeral cycle (c) and the hen's circadian cycle (b). (Morris, 1978). For practical purposes, the hen's natural cycle (b) is substituted with 24 h, so $P = p + c - 24$. The intent of this calculation was to maintain an equal effective daylength when birds are transferred between ahemeral and conventional lighting. It can be argued that the effect of ahemeral days may be caused by the increasing effective daylength that normally accompanies the increasing cycle length, rather than an effect of the ahemeral cycle. Also,

when a flock is transferred back from a period of long ahemeral cycle to conventional lighting, daylength must be increased in the conventional program in order to illuminate the hen's photosensitive phase. This is to ensure that a signal of decreasing daylength is not perceived by the bird and subsequently egg production would cease. If birds are to be returned from ahemeral to conventional lighting regimes, a practical upper limit of 14 h light in a 28 h ahemeral day would be set because this would effectively equate to 18 h of light in a 24 h conventional day. Since moving birds back from ahemeral to conventional lighting schedules is not likely in a commercial setting, this difference may be of practical significance only to researchers and in comparing different photoschedules. This idea may also contribute to the perception that long cycle lengths contribute to increased floor eggs because of the increased length of the dark period. Although Biellier and Ostmann (1960) compared timing of oviposition under ahemeral light dark cycles composed of equal periods of light and dark, little data is available on the timing of oviposition using ahemeral days while holding the length of the scotophase constant.

I.3.4 Light Intensity

Much of the recent work on light intensity has been performed using turkeys. The relationship between light intensity and reproductive traits was found to vary between different strains of large-bodied, and medium weight modern commercial turkey hens under light intensities of 18, 33 and 51 lux (Nestor and Brown, 1972). These authors suggested that optimum light intensity should be determined independently for each strain. A light intensity as low as 0.5 lux has been shown to be sufficient to cause turkey hens to lay eggs (Siopes, 1991a), although time of first oviposition was delayed. Although initiation of lay has a low light intensity threshold, it was also concluded that the effective threshold for typical onset of lay in turkeys is about 2.2 lux (Siopes, 1991a). In similar experiments, no significant differences were found in feed intake, feed efficiency or reproductive performance in turkey breeder hens housed under light intensities ranging from 54 to 324 lux (Siopes, 1991b) or on

reproductive performance using light intensities of 22 and 270 lux during the prelay and laying periods (Siopes, 1992). Fertility in turkey hens was also not affected by light intensities of 16.1 and 32.2 lux (McCartney, 1971).

The possibility that light intensity affects laying hens has been considered for many years and studies have been performed to identify the minimum light intensity required to induce a normal photoperiodic response in chickens. Dorminey *et al.* (1970) reviewed early experimentation by Roberts and Carver (1941) and Dobie *et al.* (1946) which found that if hens had 13 h of light each day, varying the light intensity from 11 to 340 lux (1 footcandle = 10.76 lux) had no effect on egg production. Experiments using laying hens in floor pens revealed no effects caused by varying light intensities between 5 to 400 lux. (Nicholas *et al.*, 1944) or benefits of even higher light levels (Ostrander *et al.*, 1960). Hughes (1973) reported that light intensities ranging from 2.2 to 10.8 lux did not affect fertility in naturally-mated, caged White Leghorns.

Other experimental results have demonstrated that light intensity can affect reproductive traits. Wilson *et al.* (1956) reported that light intensities below 4 lux retarded sexual maturation in caged pullets. Dorminey *et al.* (1970) reported that sexual maturity was delayed by 1 wk in pullets reared under 8 h of 1.1 lux (measured 15 cm above the pen floor) compared to pullets reared under 3.2, 5.4, 10.8 and 32.3 lux, and about 2 wk later than pullets reared under subdued natural light with longer day-lengths. However, light intensity had no effect on hen-day egg production, egg weight or feed efficiency. King (1962) demonstrated that pullets reared in almost complete darkness eventually became sexually mature, but produced eggs at a lower rate (59%) than those hens raised on 6 h of 5-8 lux light with weekly day-length increases of 15 min (73% average annual production).

Morris and Owen (1966) reported a logarithmic linear decline in egg production when light intensity decreased from 10 to 0.08 lux. They concluded that the minimum light intensity for maximum egg production was more than 2 but less than 10 lux, and that 0.08 lux was equivalent to darkness for photoperiodic purposes. Morris and Bhatti (1978) concluded

that the light intensity of the photophase must be at least ten times greater than intensity of the scotophase for chickens to normally entrain oviposition rhythms. Meyer *et al.* (1988) found that sexual development and activity of Japanese quail were dependent on photophase contrast rather than absolute light intensity. In this study, dim light was interpreted as darkness when brighter light was present, but was interpreted as day when the scotophase was completely dark. They also concluded that a bird's photoperiodic history did not influence whether or not it would be photostimulated with dim light. Morris (1967) demonstrated a dose response increase in egg production for hens in three-tiered cages with light intensities measured at the middle tier food trough of 0.2, 1 and 5 lux, but no further increase in egg production under 25 lux. The relationship between light intensity (0.12 to 37 lux) and egg production to 500 d of age has further been estimated by Morris as $232.4 + 15.18X - 4.256X^2$ where X is the common logarithm of light intensity in lux (Curtis, 1981).

In more recent studies using caged laying hens, no significant differences in egg production were observed with light intensity ranging from 2 to 45 lux (Hill *et al.*, 1988). Similarly, Tucker and Charles (1993) found no consistent response to light intensities from 0.5 to 15 lux, which led these authors to suggest that modern prolific hybrid laying hens may be more tolerant of low light intensities than earlier stocks. Morris (1994) concluded that the laying strains of the 1980s are less sensitive to light than those of the 1960s. Dorminey *et al.* (1970) made reference to unpublished observations which indicate that breeds may differ in their response to low light intensity. Hill *et al.* (1988) suggested that the range of intensities utilized may not have been extreme enough to produce a clear response. In a recent study at the University of Alberta using broiler breeders, no difference in sexual development was found between hens photostimulated with either 10 or 100 lux (Muller *et al.* 1996).

The light intensity threshold in chickens for the onset of reproductive function appears to be relatively low. For this reason it has been suggested that management practices supply sufficient light intensity for safe working conditions and proper inspection of stock, rather than attempt to meet the chicken's minimum physiological requirement (Morris, 1994). The results

of light intensity studies using large pens are also subject to question because the degree of illumination varies considerably with proximity to the light source. Measurements of light intensity in rearing pens (4.75 x 5.85 m) varied from 1 lux in the corners to 15 lux at floor level directly beneath the single hanging incandescent light bulb (H. Oosterhoff, unpublished data). Very little data is available on the effects of light intensity on reproductive morphology in modern strains of SCWL.

I.4 SEXUAL MATURITY

The attainment of sexual maturity is governed by body weight (BW) (Brody *et al.*, 1980, 1984) body fat (Bornstein *et al.*, 1984) body fat-free mass or lean body mass (Soller *et al.*, 1984) photoperiod (Chaney and Fuller, 1975) and age (Brody *et al.*, 1980, 1984; Dunnington *et al.*, 1984). Photostimulation with increasing daylength is known to advance age at sexual maturity, control egg size, and increase flock uniformity and rate of lay. However, in the absence of a photostimulatory increase in daylength, Lupicki (1994) found that modern Leghorns housed under a 8L:16D photoperiod would still initiate lay, although it was delayed to 22 to 23 wk of age whereas feed restricted broiler breeder hens began laying at 29 to 30 wk of age.

A typical management schedule specified for modern strains of SCWL aims for adequate growth prior to the initiation of lay, with the target age for sexual maturity at approximately 19 wk. Production levels should reach 10% by 20 wk of age and 50% production should be achieved at 21 - 22 wk of age. Peak production of 93% or higher can be reached at 26 - 28 wk of age (Anonymous, 1991; 1992; 1993).

I.5 HISTORY OF THE BREEDING INDUSTRY

Since the beginning of this century, the poultry industry has rapidly evolved into a modern highly-disciplined production system. In the early 1900's, almost every farm possessed some poultry to provide meat and eggs. Although records were not kept,

productivity was probably extremely low (Hunton, 1990). However, discoveries in the areas of nutrition, housing, and disease control began the process of intensification and concentration of the industry. Advances in communication have allowed research results to become readily available to producers. In addition, modern, high-speed transportation has allowed world-wide distribution of commercial and breeding stock from individual breeding and production units.

The main objective of breeders in the early part of the 20th century was to sell males to other breeders who supplied local hatcheries from multiplier flocks. Practical breeding until the first decade of the 20th century was dominated by chicken fanciers who selected their stock mainly on feather colour and breed type. Very little attention, if any, was dedicated to egg production (Hartmann, 1988). In Hartmann's review (1988) of the developing poultry industry, it was noted that around this time there was a change in trend to include concern for egg production traits, with contributions published by Pearl (1912), Goodale (1918) Hurst (1921) and Hays (1924). The global diversity of breeding stock was much greater than it is today, even though local genetic bases were probably less diverse because of inbreeding and the influence of only a few local breeders (Hunton, 1990).

In the late 1940's, select breeders began to develop poultry as a serious large-scale business, rather than a sideline or hobby. Once the business and improvement potential was recognized, these breeders expanded and began serious genetic selection and breeding programs. The first breeding company to employ a full time geneticist was Kimber Farms, California, when they hired Dr. W.F. Lamoreux in 1943 (Hunton, 1990).

As the commercial interests in the poultry industry grew, so did the need to test and identify superior stocks. Standard laying tests were begun and egg production was recorded for pens of birds supplied by breeders to a testing station (Hunton, 1990). However, various concerns were raised regarding the reliability of standard laying tests, such as: 1) the effect of environmental and management differences, 2) the lack of appropriate replication, and 3) questions regarding the representative nature of the stocks entered. Standard laying tests were soon replaced by random sample tests for layers, which made efforts to select adequate

numbers of representative birds at random from a breeders flock, often as chicks or hatching eggs. Publication of these results led to a convenient buyer's guide for superior stocks and was an effective stimulus for breeders to increase their efforts in stock improvement. Inevitably, this also led to fewer breeding companies and strains of chickens, as can be demonstrated by the changing participation in Random Sample Egg Production Tests of the United States and Canada (Hartmann, 1988). The number of breeders represented in the 1961/62 test period was 126 with 185 strains. This had declined to 59 breeding farms and 90 strains in the 1965/66 test period, and 20 farms with 34 strains a decade later. Data from the 1977/78 test period indicates only 17 breeding farms and 27 strains participated, and today many of these breeders have also disappeared. Most eggs are now produced by production enterprises housing layers numbering from several thousands to hundreds of thousands (Nesheim *et al.*, 1979). The changes which have occurred during the past 40 years reflect the transition of poultry production from a farming activity to a large scale industry.

I.5.1 Evidence of Progress

The progress made in poultry performance is reflected in the results from the official Random Sample Egg Production Tests. Hartmann (1988) has reported data from Random Sample Egg Production Tests in the U.S.A. and Canada that demonstrate a 40% increase in egg production from 1959 to 1978, with nearly one quarter less feed consumed per kilogram of egg mass produced (Table I-1). Although these results should generally reflect a genetic tendency, they are still phenotypic in nature and assessment of genetic improvement is limited by the lack of a control and by breeders changing genetic strains during this time period.

Hunton (1990) reported that two breeders did not change their stock designations between the period of 1961 through 1977. Select data from these two stocks and the Kentville Control which were entered continuously in a number of tests throughout this period, has previously been reported by Hunton (1990) (Table I-2). The commercial strains show an improvement in egg production of 26 and 30 eggs while the Kentville control gained only

four. Egg weight increased in the commercial strains over this time, but BW was seen to decrease.

Foster and Weatherup (1977) have estimated that the average rate of advance in egg production due to selection in commercial breeds from 1967 to 1974 was slightly greater than 1 egg per year. The argument that improvement was due to management control rather than genetics has been addressed by Dickerson and Mather (1976) who concluded that genetic improvement had occurred during the period 1958 to 1970 in commercial stocks for egg numbers (8% on floor and 14% in cage) and in live hen-day egg production (9%). McMillan *et al.* (1990) showed similar genetic improvement of 11.5% and 6.3% in 50 wk hen-housed and survivor production for the period of 1950 to 1980.

The progress in genetics and management has developed the modern SCWL into a bird capable of very efficient egg production. Management guides for various commercial strains indicate objectives for cumulative hen-housed production of 275 to 280 eggs to 68 wk of age (Anonymous, 1991, 1992, 1993). High producing SCWL may lay 300 or more eggs before 68 wk, compared to a high producing flock of feed-restricted broiler-breeder hens who have been reported to produce 184 hatching eggs to 62 wk of age (Robinson *et al.*, 1990). Evidence of genetic progress in egg weight and hen-day production are also supported by data from the random-bred strain of SCWL housed at the University of Alberta Poultry Research Unit as compared to modern targets for a typical commercial SCWL strain in Figure I-1 and I-2 (H. Oosterhoff, unpublished data).

I.5.2 Selection and Breeding Programs

Selection for egg production in commercial stocks has been the result of considerable research. The reader is referred to Arthur (1986); Fairfull and Gowe (1990) and Hunton (1990) for reviews of commercial breeding practice and genetics of egg production in chickens.

Today's global economy has developed primary breeding companies which are

involved in developing stocks to serve many markets in different parts of the world. The strategies implemented in an effort to meet producer needs differ from providing a single-versatile strain to supplying a limited range of more specialized products (Hunton, 1990). Selection pressure exerted by the various primary breeders over time has created commercial strains of modern SCWL which are claimed to differ in their response to environmental stimuli, management practice and production potential.

Although selection criteria and the importance of traits differ between breeders, there are common aspects between them as well. Egg weight, BW, egg quality traits (such as shell quality, shell colour, albumen height, and the absence of blood and meat spots) feed efficiency and disease resistance have all been identified as important in selection programs (Hunton, 1990). Egg production has always been of major importance in the selection criteria applied to layer stocks. Various methods for measuring and selecting on the basis of increased egg production have also been developed and tested. The advent of Best Linear Unbiased Prediction (BLUP) was an improvement of multi-trait index selection and considers the additive genetic relationship among all animals considered (Hunton, 1990). This tool allows for complex economic and genetic assessment.

Two added selection problems associated with poultry breeding have been identified by Fairfull and Gowe (1990). First, the commercial egg production hen is a strain or breed cross. Selection within the pure parental lines does not necessarily select for individuals needed to optimize nonadditive gene action within their progeny, so reciprocal recurrent selection (RRS) is sometimes used. RRS does not maximize the performance of the parental lines but is a form of family selection that uses data from reciprocal crosses to select pure line parents. The second problem found in layer development is that primary breeder's pure strain hens are housed individually in cages while hens housed by commercial operations are generally housed in multiple-hen cages. Muir and Ligget (1995ab), Craig and Muir (1995) and Hester *et al.* (1995abc) have shown there may be merit in group selection for adaptation to multiple-hen cages.

I.5.3 Selection Criteria

The use of a partial egg record early in lay as a selection criterion for improving annual egg production was proposed in order to decrease the generation interval and maximize genetic improvement (Dempster and Lerner, 1947). Oliver *et al.* (1957) indicated that genetic gains should be more rapid using partial egg record rather than annual record. The parameter estimates they obtained led to the conclusion that selection on percent production of the partial record would result in greater improvement than selection for number of eggs to a fixed date. Selection for part-record egg numbers or rate of lay resulted in increased egg production in Saadeh *et al.* (1968), Kinney *et al.* (1970), Bohren *et al.* (1970), Poggenpoel and Erasmus (1978), Lowe and Garwood (1980), and Boukila *et al.* (1987). However, Gowe and Strain (1963) concluded that although improvements in partial record were realized, no gain in annual production occurred after a few generations of multi-trait selection using partial egg production records and egg weight. Their work implies that increased early production is countered by equivalent production decreases in the remainder of the laying period. Ibe *et al.* (1982) found that although selection for part record rate of egg production showed significant positive correlated responses for full record rate of lay and egg number, there was a response limit after the 12th generation, with a lack of positive response thereafter.

While gains in part-record and annual production have been shown as a result of selection for increased egg numbers during the early part-record, one secondary affect seems to be a reduction in age at sexual maturity (Apblanalp *et al.*, 1964). A decrease in egg weight appears also to be a result of selection for short term rate of egg production (Saadeh *et al.*, 1968; Bohren *et al.*, 1970; Kinney *et al.*, 1970; Craig *et al.*, 1969). This limits the practical value of selection for part-record egg production as a sole selection criterion because most producers are paid differentially according to egg size. It has been reported that when egg weight is included as a criterion in multiple-trait selection, no reduction in age at sexual maturity was observed and therefore the contribution of earlier production to increased early part record egg numbers was eliminated (Gowe and Strain, 1963). Jackson *et al.* (1986) found

that multi-trait selection for high egg production and other commercially important traits increased the efficiency of egg production and influenced egg composition.

Lowe and Garwood (1980) concluded that indentification of a part record after 30 wk of age, consisting of four consecutive weeks, would provide a reasonably good basis for selection to improve annual rate of lay. In two of three strains of White Leghorns, Boukila *et al.* (1987) demonstrated that improvements in annual egg production could be achieved using selection on the early partial record egg number or percent production (21 to 30, 34 or 38 wk), instead of selection using the complete part record (21 to 42 wk). However, these authors also concluded that selection on only the earliest part of lay may contribute to decreased persistency throughout the remainder of the production cycle.

Bohren *et al.* (1981) reported a consistent and significant increase in number of eggs to 40 wk under 3 yr selection for early sexual maturity. However, no correlated response was observed in percent production to 40 wk, annual percent production, or annual number of eggs produced. These data also demonstrate that gains in early egg numbers from early sexual maturity do not necessarily contribute to increased total egg production or production rate.

Selection for reduced time interval between ovipositions has been previously reported (McClung *et al.*, 1976; Gow *et al.*, 1985; Yoo *et al.*, 1986). Yoo *et al.* (1986) found the rate of lay to 301 d of age increased linearly by 6.3% for each hour decrease in mean intra-sequence interval with a limit at 24 h under a 14L:10D photoperiod. However, McClung *et al.* (1976) found no significant parallel change in annual egg production because the effect of the longer sequences which resulted from selection for shorter intra-sequence interval was offset by longer pauses. Although Zakaria *et al.* (1984b) reported on the relationship of clutch length to ovarian follicular growth, there appears to be a lack of data reporting on the relationship of egg production and sequence profiles to ovarian morphology in strains of SCWL which have been developed under different selection criteria.

Selection for feed efficiency has also been studied in recent years. One aspect of layer profitability can be expressed in terms of income minus feed cost (IFC) and deserves the

attention of breeders because it is an important trait for the economic success of the producer (Hagger, 1990). Residual feed consumption (RFC) in laying hens, defined as the difference between observed feed intake and intake estimated from BW, egg mass produced, and change in BW (Hagger, 1991, 1994), have been suggested as methods to select for feed efficiency. Bordas *et al.* (1992) has shown that selection for negative residual feed consumption has improved feed efficiency using Rhode Island Red laying hens. Although RFC and %RFC have been shown to be moderately to highly heritable (Luiting and Urff, 1991; Katle and Kolstad, 1991), Hagger (1994) found no genetic correlation between RFC and IFC. RFC was found to be of only limited value as an additional selection trait to improve IFC because BW and the production of egg mass substantially contribute to IFC, and therefore RFC would contribute very little additional genetic correlation to this trait (Hagger, 1994). However, Schulman *et al.* (1994) observed a genetic correlation between RFC and feed consumption of 0.50 (±0.04). Feed consumption was decreased in this Finnish egg-layer population through four generations of selection for RFC, with no change found in egg mass, number of eggs, egg weight, age at first egg, or BW (Schulman *et al.*, 1994). This would indicate that selection for RFC could be effective in increasing the profitability of layer stocks.

I.5.4 Associated Problems

Selection for earlier sexual maturity and increased egg size are opposing ideals. Research has shown that earlier sexual maturity is related to increased production of small eggs (Harrison *et al.*, 1969; Bell *et al.*, 1982). This is likely because sexual maturity occurs when pullets are actively growing and sexual maturity and aspects of BW are closely related (Brody *et al.*, 1980; 1984; Bornstein *et al.*, 1984; Soller *et al.*, 1984). Therefore, with a reduction in age at sexual maturity, we might also expect a reduction in BW and this has been shown to influence early egg size (Summers and Leeson, 1983). This would seem to be supported by selection for partial egg numbers which generally results in reduced age at sexual maturity and reduced egg size (Saadeh *et al.*, 1968; Bohren *et al.*, 1970; Kinney *et al.*, 1970;

Craig *et al.*, 1969) However, selection programs have successfully included the criteria of increased egg size and weight with early sexual maturity (Hunton, 1990). This has created secondary problems associated with smaller birds and larger eggs. A study conducted by Robinson (1993) found that mortality in Alberta's layer flocks was primarily the result of oviductal prolapse. This author also identified other causes of mortality which included internal laying, fatty liver haemorrhagic syndrome and complications related to these reproductive disorders. Flocks with the higher incidences of reproductive problems contributing to mortality also produced heavier eggs (+3 g). This was interesting as it suggested that BW-related reproductive problems similar to those found in overweight broiler-breeder hens can be found in layer flocks as well.

Selection for feed efficiency has a downward selection pressure on feed intake, as previously described. Increased egg mass output from smaller hens, however, requires increased intake to supply the energy, protein and calcium demands of high production rates over extended periods of time. This increased demand for nutrients, complicated by decreased dietary intake will necessitate the use of feeds which are higher in nutrient concentration. Failure to supply a diet sufficient in all nutrients inevitably leads to lower egg production, metabolic disorders such as cage layer fatigue (osteoporosis) and eventually cessation of lay or death. Robinson (1993) reported that cage layer fatigue comprised 3.53% of non-infectious mortality in the Alberta layer flocks studied. Over 75% of deaths in the flock with the highest mortality were caused by metabolic disease and this flock also had the highest incidence of reproductive problems. Overall, two-thirds of mortality was attributed to reproductive and metabolic disorders.

Robinson *et al.* (1996) proposed that pullets with inadequate body reserves may have a compromised ability to reach high peak production, and body reserves which they do possess may become quickly depleted. Similarly, production of large eggs from small hens may jeopardize hen health from increased reproductive and metabolic disorders (Robinson, 1993). Recent scientific data is limited on any differences between SCWL strains for production and

morphological traits under similar management practices. In order to maximize production of modern strains of SCWL, management practices which are highly specific may be required.

I.6 RESEARCH OBJECTIVES

All of these reports serve to emphasize that the modern SCWL is a highly specialized bird selected for high egg production and efficiency. The objective of the first chapter of this thesis is to provide a summary of the current state of knowledge of avian reproductive physiology, egg-layer management, and trends in genetic selection for egg production stocks. The hypothesis of the research conducted here is that significant strain differences exist in SCWL which have been developed under different selection pressures in terms of ovarian morphology, carcass traits, egg production traits, and response to their environment.

I.6.1 Project Descriptions

Experiment 1. The specific objectives of this research is to determine if commercial strains of SCWL developed under different selection programs of different primary breeders would differ in age at sexual maturity and BW, and to determine if these differences influence ovarian morphology, reproductive organ development, carcass traits, egg production and laying patterns. The relationship between ovarian morphology at sexual maturity and end of lay with production profiles will also be investigated.

Experiment 2. This project is designed to examine the effects of light intensity of photostimulation on the age of sexual maturity, ovarian morphology, reproductive and carcass traits in both a modern commercial strain and a random-bred "antique" strain of SCWL. Significant interactions between the main effects, light intensity and strain, were also studied.

I.7 TABLES AND FIGURES

Table I-1. Average egg production and efficiency of food conversion of laying hens to 500 d of age in combined summaries of Random Sample Egg Production Tests in United States and Canada (1949 - 78) and Europe (1978 and 1984). (As reported by Hartmann, 1988)

	Egg Production per hen housed		Food consumption per kg egg mass	
Period	Eggs	Rel.	Kg	Rel.
US and Canada[1]				
1949/50	175	100	3.40	100
1959/60	213	122	2.95	87
1969/70	219	125	2.75	81
1977/78	243	139	2.60	76
Europe[2]				
1978	260	100	2.73	100
1984	276	106	2.52	92

[1] Data from Report No. 1: California Random Sample Test 1949-50 and USDA Reports 1959 - 79.
[2] Data from Working Group No. 3 (1981, 1986).

Table I-2. Changes in selected traits in egg stocks measured in North America random sample tests from 1961-63 to 1975-77. (As reported by Hunton, 1990)

Trait	Age at 50% production (d)		Eggs per hen housed		Egg weight (g)		BW (g)	
Time Period	1961-3	1975-7	1961-3	1975-7	1961-3	1975-7	1961-3	1975-7
Commercial Stock 1	173	164	234	260	59.4	62.0	2177	1874
Commercial Stock 2	169	164	232	252	58.9	60.6	2132	1760
Kentville Control	174	169	213	217	58.9	58.5	2132	1919

Data are regressed means taken from 1963 and 1977 Report of Random Sample Egg Production Test, United States and Canada, U.S.D.A.

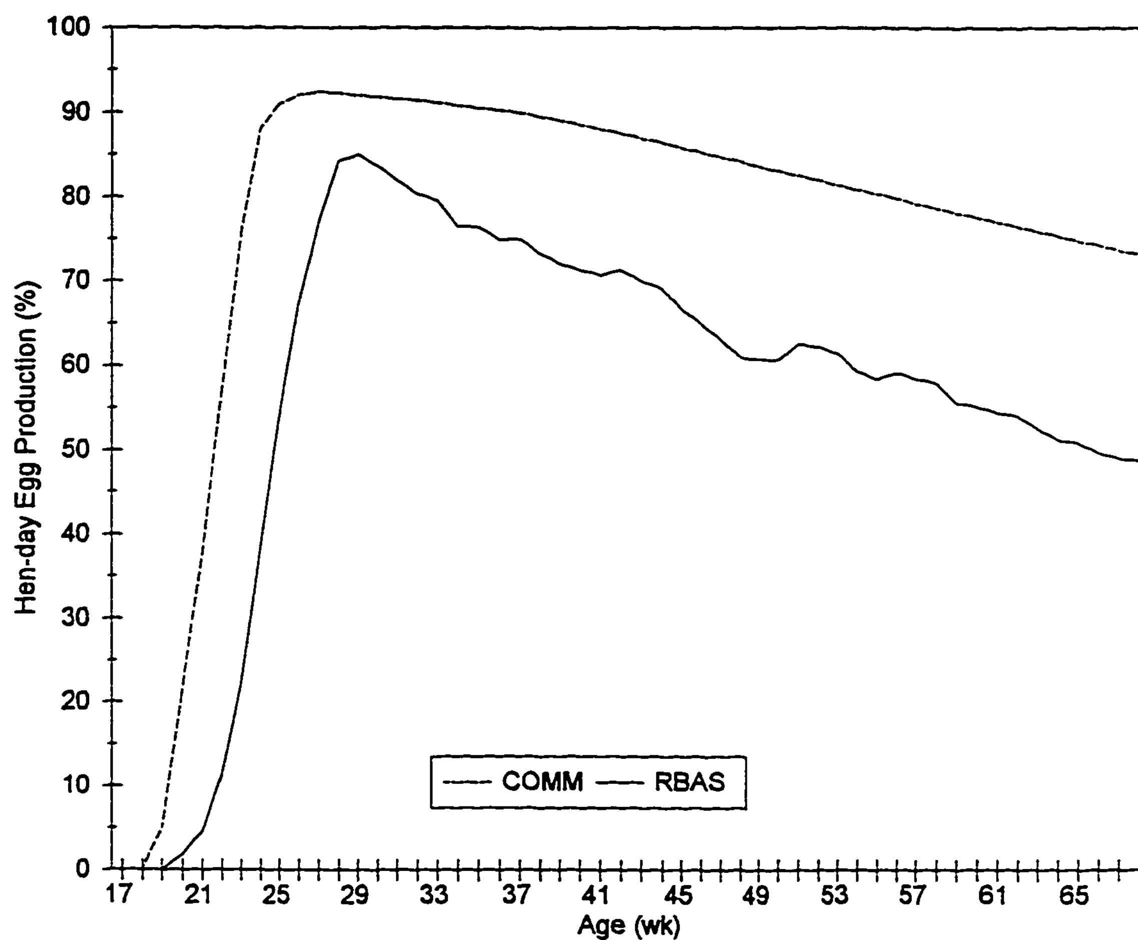

Figure I-1. **Hen-day egg production curves of target for typical modern commercial strain (COMM[1]) and collected data (1995) of an antique random-bred control strain (RBAS[2]; n=70) of Single Comb White Leghorn hen**

[1] COMM = Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

[2] RBAS = University of Alberta Random-bred Antique Strain

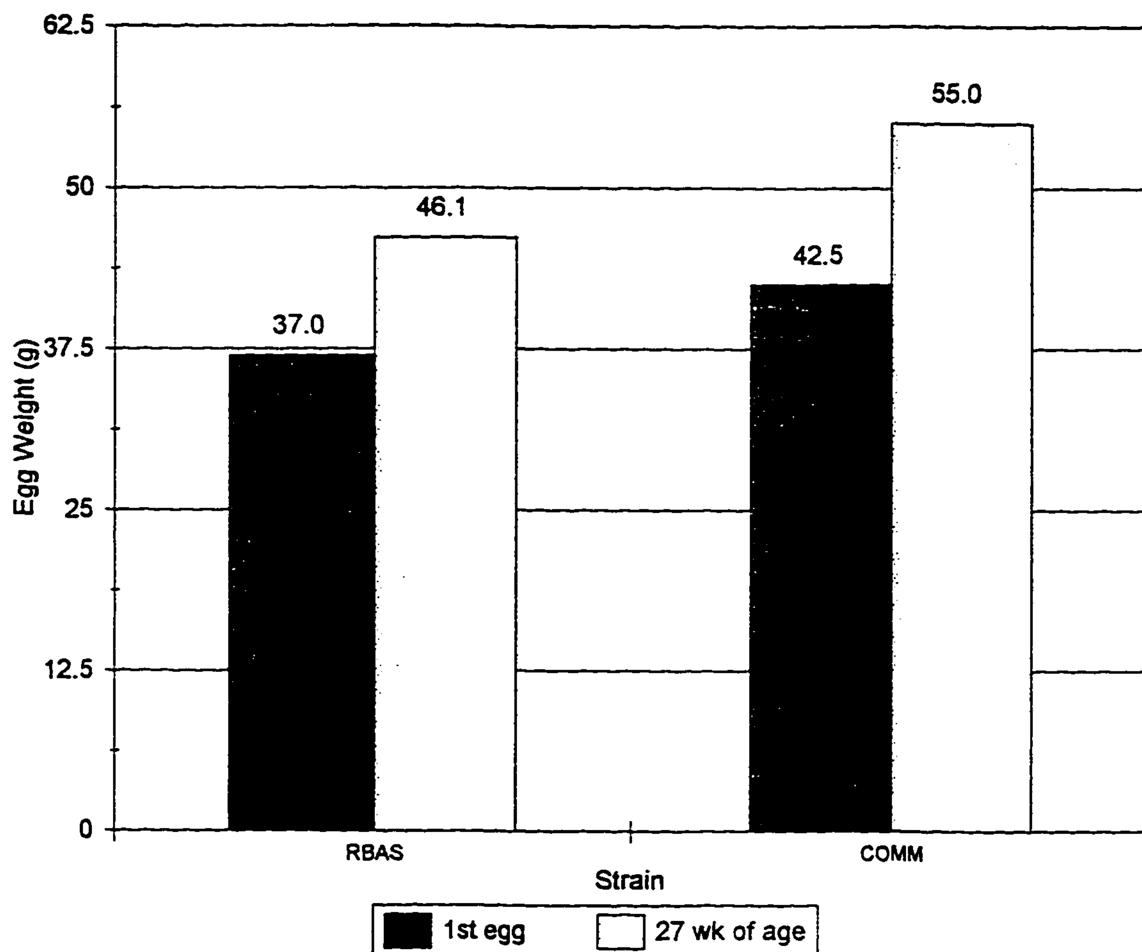

Figure I-2. **Egg weight at first oviposition and at 27 wk of age for a typical modern commercial strain target (COMM[1]) and collected data (1995) of an antique random-bred control strain (RBAS[2]; n=70) of Single Comb White Leghorn hen**

[1] COMM = Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

[2] RBAS = University of Alberta Random-bred Antique Strain

I.8 REFERENCES CITED

Advis, J.P., and A.M. Contijoch, 1993. The median eminence as a site for neuroendocrine control of reproduction in hens. Poultry Sci. 72: 932-939.

Anonymous, 1991. Shaver White Commercial Management Guide (T-05-I), Shaver Poultry Breeding Farms Limited, Cambridge, Ontario, Canada N1R 5V9.

Anonymous, 1992. Shaver Starcross 288 Commercial Management Guide, Shaver Poultry Breeding Farms Limited, Cambridge, Ontario, Canada N1R 5V9.

Anonymous, 1993. ISA Babcock B 300 White Egg Layer Management Guide, North America - 1993 edition. ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY 14851.

Anonymous, 1997. Eggnotes: March, 1997 Newsletter, Alberta Egg Producers Board, 15 1915 32 Ave NE, Calgary , AB.

Apblanalp, H., D.C. Lowry, I.M. Lerner, and E.R. Dempster, 1964. Selection for egg numbers with X-ray induced variation. Genetics 50. 1083-1100.

Arthur, J.A., 1986. An evaluation of industry breeding programs for egg type chickens. Proc. 3rd World Congr. Genet. Appl. Livestock Production. (Lincoln) 10: 325-336.

Bell, D.D., D.R. Kuney, and C.J. Adams, 1982. Varying the age of sexual stimulation in SCWL pullets. Poultry Sci. 61: 1416 (Abstr.).

Bhatti, B.M., and T.R. Morris, 1978a. Entrainment of oviposition in the fowl using light/dark cycles. Br. Poult. Sci. 19: 333-340.

Bhatti, B.M., and T.R. Morris, 1978b. The relative importance of sunrise and sunset for entrainment of oviposition in the fowl. Br. Poult. Sci. 19: 365-371.

Biellier, H.V., and O.W. Ostmann, 1960. Effect of varying day length on time of oviposition in domestic fowl. Res. Bull. Missouri Agric. Exp. Stn. No. 747.

Bohren, B.B., V.A. Garwood, and P.C. Lowe, 1981. Direct and correlated responses to selection for age at maturity in the fowl. Poultry Sci. 60: 289-294.

Bohren, B.B., T.B. Kinney, S.P. Wilson, and P.C. Lowe, 1970. Genetic gains in annual egg production from selection on part-record percent production in fowl. Genetics 65: 655-667.

Bordas, A., M. Tixier-Boichard, and P. Mérat, 1992. Direct and correlated responses to divergent selection for residual food intake in Rhode Island Red laying hens. Br. Poult. Sci. 33: 741-754.

Bornstein, S., I. Plavnik, and Y. Lev, 1984. Body weight and/or fatness as potential determinants of the onset of egg production in broiler breeder hens. Br. Poult. Sci. 25: 323-341.

Boukila, B., M. Desmarais, J.P. Pare, and D. Bolamba, 1987. Selection for increased egg production based on annual record in three strains of white leghorns. 1. Comparison of different partial records to improve annual egg production. Poultry Sci. 66: 1077-1084.

Brody, T., Y. Eitan, M. Soller, I. Nir, and Z. Nitsan. 1980. Compensatory growth and sexual maturity in broiler females reared under severe food restriction from day of hatching. Br. Poult. Sci. 21: 437-446.

Brody, T.B., P.B. Siegel, and J.A. Cherry, 1984. Age, body weight, and body composition requirements for the onset of sexual maturity of dwarf and normal chickens. Br. Poult. Sci. 25: 245-252.

Burke, W.H., 1984. Avian reproduction. pp 847-862. *in:* Duke's Physiology of Domestic Animals, 10th edition, Swanson, M.J., ed. Cornell University Press, New York, NY.

Burke, W.H., and P.T. Dennison, 1980. Prolactin and luteinizing hormone levels in female turkeys (*Meleagris gallopavo*) during a photoinduced reproductive cycle and broodiness. Gen. Comp. Endocrinol. 41: 92-100.

Byerly, T.C., and O.K. Moore, 1941. Clutch length in relation to period of illumination in the domestic fowl. Poultry Sci. 20: 387-390.

Cahaner, A., and H. Abplanalp, 1979. Changes in egg production and egg intervals under selection for high egg number under 22 hour day cycles of artificial lighting. Poultry Sci. 58: 757-761.

Chaney, L.W., and H.L. Fuller, 1975. The relationship of obesity to egg production in broiler breeder pullets. Poultry Sci. 54: 200-207.

Clunies, M., D. Parks, and S. Leeson, 1992. Calcium and phosphorus metabolism and eggshell formation of hens fed different amounts of calcium. Poultry Sci. 71: 482-489.

Craig, J.V., D.K. Biswas, and H.K. Saadeh, 1969. Genetic variation and correlated responses in chickens selected for part-year rate of egg production. Poultry Sci. 48: 1288-1296.

Craig, J.V., and W.M. Muir, 1995. Group selection for adaptation to multiple-hen cages: Cannibalistic deaths and feather condition. Poultry Sci. 74 (Suppl. 1): 101 (Abstr.).

Curtis, S.E., 1981. Environmental Management in Animal Agriculture. Animal Environment Services, Mahomet, IL.

Day, S.L., and A.V. Nalbandov, 1977. Presence of prostaglandin F (PGF) in hens follicles and its physiological role in ovulation and oviposition. Biol. Reprod. 16: 486-494.

Dempster, E.R., and I.M. Lerner, 1947. The optimum structure of breeding flocks 1. Rate of genetic improvement under different breeding plans. Genetics 32: 555-566.

Dickerson, G.E., and F.B. Mather, 1976. Evidence concerning genetic improvement in commercial stocks of layers. Poultry Sci. 55: 2327-2342.

Dobie, J.B., J.S. Carver, and J. Roberts, 1946. Poultry lighting for egg production. Washington Agri. Exper. Sta. Bull. No. 471.

Dorminey, R.W., J.E. Parker, and W.H. McClusky, 1970. Effect of light intensity on leghorn pullets during the development and laying periods. Poultry Sci. 49: 1657-1661.

Dunn, I.C., and P.J. Sharp, 1990. Photoperiodic requirements for LH release in juvenile broiler and egg-laying strains of domestic chicken fed *ad libitum* or restricted diets. J. Reprod. Fertil. 90: 329-335.

Dunnington, E.A., P.B., Siegel, and J.A. Cherry, 1984. Delayed sexual maturity as a correlated response to selection for reduced body weight in White Plymouth Rock pullets. Arch. Geflugelkd. 48: 111-113.

Etches, R.J., 1979. Plasma concentrations of progesterone and corticosterone during the ovulation cycle of the hen (*Gallus domesticus*). Poultry Sci. 58: 211-216.

Etches, R.J., 1987. Calcium logistics in the laying hen. J. Nutr. 117: 619-628.

Etches, R.J., 1990. The ovulatory cycle of the hen. CRC Crit. Rev. Poult. Biol. 2: 293-318.

Etches, R.J., 1996. Reproduction in Poultry. CAB International. Wallingford, UK.

Etches, R.J., H.E. MacGregor, T.R. Morris, and J.B. Williams, 1983. Follicular growth and maturation in the domestic hen (*Gallus domesticus*). J. Reprod. Fertil. 67: 351-358.

Etches, R.J., J.N. Petitte, and C.E. Anderson-Langmuir, 1984. Interrelationships between the hypothalamus, pituitary gland, ovary, adrenal gland, and the open period for LH release in the hen (*Gallus domesticus*). J. Exp. Zool. 232: 501-511.

Etches, R.J., and J.P. Schoch, 1984. A mathematical representation of the ovulatory cycle of the domestic hen. Br. Poult. Sci. 25: 65-76.

Fairfull, R.W., and R.S. Gowe, 1990. Genetics of egg production in chickens. pp 705-760. *in:* Poultry Breeding and Genetics. R.D. Crawford, ed. Elsevier, Amsterdam.

Follett, B.K., 1985. The environment and reproduction. pp. 103-132 *in*: Reproduction in Mammals. C.R. Austin and R.V. Short, ed. Univ. Press, Cambridge, London.

Foster, R.G., and B.K. Follett, 1985. The involvement of rhodopsin-like photopigment in the photoperiodic response of the Japanese quail. J. Comp. Physiol. A. 157: 519-528.

Foster, W.H., and S.T.C. Weatherup, 1977. An estimation of the advances achieved over seven years of selection within commercial egg-laying breeds. Wld's Poultry Sci. J. 33: 133-139.

Fraps, R.M., 1955. Egg production and fertility in poultry. p 661. *in*: Progress in the Physiology of Farm Animals, vol. 2., Hammond, J., ed. Buttorworths Scientific, London.

Freeman, B.M., 1984. Appendix: Biochemical and physiological data. pp. 407-424 *in:* Physiology and Biochemistry of the Domestic Fowl. vol. 5., Freeman, B.M., ed. Academic Press, London.

Gilbert, A.B., 1971. The ovary. pp 1163-1208. *in*: Physiology and Biochemistry of the Domestic Fowl, Vol. 3. Bell, D.J., and B.M. Freeman, ed. Academic Press, London.

Gilbert, A.B., J. Peddie, G.G. Mitchell, and P.W. Teague, 1981. The egg-laying response of the domestic hen to variation in dietary calcium. Br. Poult. Sci. 22: 537-548.

Gilbert, A.B., M.M. Perry, D. Waddington, and M.A. Hardie, 1983. Role of atresia in establishing the follicular hierarchy in the ovary of the domestic hen (*Gallus domesticus*). J. Reprod. Fertil. 69: 221-227.

Gilbert, A.B., and J.W. Wells, 1984. Structure and function of the ovary. pp 15-27. *in*: Reproductive Biology of Poultry, Cunningham, F.J., Lake, P.E., and D. Hewitt, eds. British Poultry Science Ltd.

Goodale, H.D., 1918. Internal factors influencing egg production in the Rhode Island Red breed of domestic fowl. American Naturalist, 52: 65-94, 209-232, 301-321.

Gow, C.B., P.J. Sharp, N.B. Carter, R.J. Scaramuzzi, B.L. Sheldon, B.H. Yoo, and R.T. Talbot., 1985. Effects of selection for reduced oviposition interval on plasma concentrations of luteinizing hormone during the ovulatory cycle in hens on a 24 h lighting cycle. Br. Poult. Sci. 26: 441-451.

Gowe, R.S., and J.H. Strain, 1963. Effect of selection for increased egg production based on part-year records in two strains of White Leghorns. Can. J. Genet. and Cytol. 5: 99-100 (Abstr.).

Hagger, C., 1990. Response from selection for income minus food cost in laying hens, estimated via the animal model. Br. Poult. Sci. 31: 701-713.

Hagger, C., 1991. Phenotypic and genetic effects on feed intake of laying hens in different years. Poultry Sci. 70: 434-439.

Hagger, C., 1994. Relationships between income minus feed cost and residual feed consumption in laying hens. Poultry Sci. 73: 1341-1344.

Hammond, R.W., D.M. Olson, R.B. Frenkel, H.V. Biellier, and F. Hertelendy, 1980. Prostaglandins and steroid hormones in plasma and ovarian follicles during the ovulation

cycle of the domestic hen (*Gallus domesticus*). Gen. Comp. Endocrinol. 42: 195-202.

Hargrove, T.L., and M.A. Ottinger, 1992. Induced oviposition of precalcified eggs following prostaglandin administration. Poultry Sci. 71: 548-552.

Harrison, P.C., 1972. Extraretinal photocontrol of reproductive responses of leghorn hens to photoperiods of different length and spectrum. Poultry Sci. 51: 2060-2064.

Harrison, P.C., 1974. Spectrum influence on extraretinal control of daily oviposition cycles. Poultry Sci. 53:560-564.

Harrison, P.C., G. Schmaier, and J. McGinnis, 1969. Reproductive development and response of White Leghorn pullets subjected to increasing daylengths at different ages. Poultry Sci. 48: 1021-1026.

Hartmann, W., 1988. From Mendel to multi-national in poultry breeding. Br. Poult. Sci. 29: 3-26.

Hays, F.A., 1924. Inbreeding the Rhode Island Red fowl with special reference to winter egg production. American Naturalist, 58: 43-59.

Hertelendy, F., and T.G. Taylor, 1961. Changes in blood calcium associated with egg shell calcification in the domestic fowl. 1. Changes in the total calcium. Poultry Sci. 40: 108-114.

Hester, P.Y., W.M. Muir, J.V. Craig, and J.L. Albright, 1995a. Group selection for adaptation to multiple-hen cages: Response to social and cold stress. Poultry Sci. 74 (Suppl. 1): 102 (Abstr.).

Hester, P.Y., W.M. Muir, J.V. Craig, and J.L. Albright, 1995b. Group selection for adaptation to multiple-hen cages: Response to social and heat stress. Poultry Sci. 74 (Suppl. 1): 102 (Abstr.).

Hester, P.Y., W.M. Muir, and J.V. Craig, 1995c. Group selection for adaptation to multiple-hen cages: Immunological response to social, cold, and heat stress. Poultry Sci. 74 (Suppl. 1): 102 (Abstr.).

Hester, P.Y., N.F. Newlon, and P.M. Klingensmith, 1991. Plasma, follicular, and uterine levels of prostaglandins in chickens laying soft-shelled and shell-less eggs. Poultry Sci. 70: 1585-1593.

Hill, J.A., D.R. Charles, H.H. Spechter, R.A. Bailey and A.J. Ballantyne., 1988. Effects of multiple environmental and nutritional factors on laying hens. Br. Poult. Sci 29: 499-511.

Hocking, P.M., A.B. Gilbert, M.A. Walker, and D. Waddington, 1987. Ovarian follicular structure of white leghorns fed *ad libitum* and dwarf and normal broiler breeders fed *ad libitum* or restricted to point of lay. Br. Poult. Sci. 28: 493-506.

Hocking, P.M., D. Waddington, M.A. Walker, and A.B. Gilbert, 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. Br. Poult. Sci. 30: 161-173.

Homma, K., Z. McFarland, and W.O. Wilson, 1967. Response of the reproductive organs of Japanese quail to pinealectomy and melatonin injection. Poultry Sci. 46: 314-319.

Homma, K., M. Ohta, and Y. Sakakibara, 1980. Surface and deep photoreceptors in photoperiodism in birds. pp. 149-156 *in*: Biological Rhythms in Birds: Neural and Endocrine Aspects. Tanabe, Y., K. Tanaka, and T. Ookawa, eds. Springer-Verlag, New York.

Homma, K., W.O. Wilson, and T.D. Siopes, 1972. Eyes have a role in photoperiodic control of sexual activity in coturnix. Science 178: 421-423.

Hughes, B.L., 1973. Effect of light intensity on fertility of naturally-mated white leghorns. Poultry Sci. 52: 1968-1969.

Hunton, P., 1990. Industrial breeding and selection. pp. 985-1028. *in*: Poultry Breeding and Genetics. R.D. Crawford, ed. Elsevier, Amsterdam.

Hurst, C.C., 1921. The genetics of egg production in White Leghorns and White Wyandottes, and its application to poultry breeding. 1st Wld's Poultry Congr., The Hague, pp. 3-20.

Ibe, S.N., J.J. Rutledge, and W.H. McGibbon, 1982. Curvilinear trends in direct and some correlated responses to nineteen generations of selection for part record rate of egg production in a randombred line of chickens. Poultry Sci. 61: 821-828.

Jaap, R.G., and F.V. Muir, 1968. Erratic oviposition and egg defects in broiler-type pullets. Poultry Sci. 47: 417-423.

Jackson, M.E., G.W. Friars, J.S. Gavora, C.Y. Lin, R.S. Gowe, I. McMillan, and E.T. Moran, 1986. Comparisons of control and selected strains, strain crosses, and commercial stocks of leghorns for egg production efficiency. Poultry Sci. 65: 16-25.

John, T.M., J.C. George, and R.J. Etches, 1986. Influence of subcutaneous melatonin implantation on gonadal development and on plasma levels of luteinizing hormone, testosterone, estradiol and corticosterone in the pigeon. J. Pineal Res. 3: 169-179.

Johnson, A.L., 1986. Reproduction in the female. pp. 432-451 *in*: Avian Physiology. P.D. Sturkie, ed. Springer-Verlag, New York.

Johnson,, A.L., 1990. Steroidogenesis and actions of steroids in the hen ovary. CRC Crit. Rev. Poult. Biol. 2: 319-346.

Johnson, A.L., 1993. Regulation of follicle differentiation by gonadotropins and growth factors. Poultry Sci. 72: 867-873.

Johnson, A.L., and A. van Tiehnhoven, 1980. Plasma concentrations of six steriods and LH during the ovulatory cycle of the hen, *Gallus domesticus*. Biol. Reprod. 23: 386-393.

Johnson, A.L., and A. van Tiehnhoven, 1984. Effects of aminogluthemide on luteinizing hormone and steroid secretion, and ovulation in the hen (*Gallus domesticus*). Endocrinology 114: 2276-2283.

Katle, J., and N. Kolstad, 1991. Selection for efficiency of food utilisation in laying hens: Direct response in residual food consumption and correlated responses in weight gain, egg production and body weight. Br. Poult. Sci. 32: 939-953.

Keshavarz, K., and S. Nakajima, 1993. Re-evaluation of calcium and phosphorus requirements of laying hens for optimum performance and eggshell quality. Poultry Sci. 72: 144-153.

King, D.F., 1962. Egg production of chickens raised and kept in darkness. Poultry Sci. 41: 1449.

Kinney, T.B. Jr., B.B. Bohren, J.V. Craig, and P.C. Lowe, 1970. Responses to individual, family or index selection for short term rate of egg production in chickens. Poultry Sci. 49: 1052-1064.

Leeson, S., and J.D. Summers, 1991. Commercial Poultry Nutrition. University Press, Guelph, Canada.

Lewis, P.D., G.C. Perry, T.R. Morris, and M.M. Midgley, 1992. Intermittent lighting regimes and mortality rates in laying hens. Wld's Poultry Sci. J. 48: 113-120.

Lowe, P.C., and V.A. Garwood, 1980. Efficiency of selection based on segments of the early record for improving annual rate of lay. Poultry Sci. 59: 677-680.

Lu, J., M.J. Zoran and V.M. Cassone, 1995. Daily and circadian variation in the electroretinogram of the domestic fowl: effects of melatonin. J. Comp. Physiol. A. 177: 299-306.

Luck, M.R., and C.G. Scanes, 1979. The relationship between reproductive activity and blood calcium in the calcium-deficient hen. Br. Poultry Sci. 20: 559-564.

Luiting, P. and E.M. Urff, 1991. Residual feed consumption in laying hens. 2. Genetic variation and correlations. Poultry Sci. 70: 1663-1672.

Lupicki, M.E., 1994. Ovarian morphology and steroidogenesis in domestic fowl (*Gallus domesticus*): Effects of aging, strain, photostimulation program and level feeding. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Majsa, Z., K. Mihály, and P. Péczely, 1976. Circadian rhythm of hypothalamo-hypophyseal-adrenal activity in the chicken. Acta Physiol. Acad. Sci. Hung. 47: 101-109.

Majsa, Z., and P. Péczely, 1976. Seasonal rhythm in the hypothalamo-hypophyseal-adrenal function of the chicken. Acta Physiol. Acad. Sci. Hung. 47: 111-115.

Marks, H.L., L.M. Lucas, and E.F. Godfrey, 1968. Selection for egg production in the domestic fowl under normal and "short day" environments. Poultry Sci. 47: 1170-1176.

Masuda, S., K Wakabayashi, and O. Koga, 1984. Change in the properties of follicle stimulating hormone like gonadotropin binding sites in the follicles of the hen during follicular growth. Jap. J. Zootechnical Sci. 55: 399-408.

McCartney, M.G., 1971. Reproduction of turkeys as affected by age at lighting and light intensity. Poultry Sci. 50: 661-662.

McClung, M.R., A.B.S. Wang, and W.T. Jones, 1976. Response to selection for time interval between ovipositions in the hen. Poultry Sci. 55: 160-171.

McMillan, I., R.W. Fairfull, R.S. Gowe, and J.S. Gavora, 1990. Evidence for genetic improvement of layer stocks of chickens during 1950-80. Wld's Poultry Sci. J. 46: 235-245.

Meddle, S.L., and B.K. Follett, 1995. Photoperiodic activation of Fos-like immunoreactive protein in neurones within the tuberal hypothalamus of Japanese quail. J. Comp. Physiol. A. 176: 79-89.

Menaker, M., and H. Keatts, 1968. Extraretinal light perception in the sparrow. 2. Photoperiodic stimulation of testes growth. Proc. Natl. Acad. Sci. USA 60: 146-151.

Menaker, M., R. Roberts, J. Elliott, and H. Underwood, 1970. Extraretinal light perception in the sparrow. 3. The eyes do not participate in photoperiodic photoreception. Proc. Natl. Acad. Sci. USA 67: 320-325.

Meyer, W.E., J.R. Millam, and F.A. Bradley, 1988. Photostimulation of Japanese quail by dim light depends upon photophase contrast, not light intensity. Biol. Reprod. 38: 536-543.

Midgley, M.M., T.R. Morris, and E.A. Butler, 1988. Experiments with the Biomittent lighting system for laying hens. Br. Poult. Sci. 29: 333-342.

Mitchell, M.E., 1970. Treatment of hypophysectomised hens with partially purified avian FSH. J. Reprod. Fertil. 22: 223-241.

Moore, R.Y., 1983. Organization and function of a central nervous system circadian oscilator: the suprachiasmatic hypothalamic nucleus. Fed. Proc. 42: 2783-2789.

Moran, E.T. Jr., 1987. Protein requirement, egg formation and the hen's ovulatory cycle. J. Nutr. 117: 612-618.

Morris, T.R., 1967. The effect of light intensity on growing and laying pullets. Wld's Poultry Sci. J. 23: 246-252.

Morris, T.R., 1973. The effects of ahemeral light and dark cycles on egg production in the fowl. Poultry Sci. 52: 423-445.

Morris, T.R., 1978. The photoperiodic effect of ahemeral light-dark cycles which entrain circadian rhythms. Br. Poult. Sci. 19: 207-212.

Morris, T.R., 1994. Lighting for layers: what we know and what we need to know. Wld's Poultry Sci. J. 50: 283-287.

Morris, T.R., and B.M. Bhatti, 1978. Entrainment of oviposition in the fowl using bright and dim cycles. Br. Poult. Sci. 19: 341-348.

Morris, T.R., M.M. Midgley, and E.A. Butler, 1990. Effect of age at starting Biomittent lighting on performance of laying hens. Br. Poult. Sci. 31: 447-455.

Morris, T.R., and V.M. Owen, 1966. The effect of light intensity on egg production. Proc. 13th Wld's Poultry Congress, pp. 458-461.

Muir, W.M., and D. Liggett, 1995a Group selection for adaptation to multiple-hen cages: Selection program and responses. Poultry Sci. 74 (Suppl. 1): 101 (Abstr.).

Muir, W.M., and D. Liggett, 1995b. Group selection for adaptation to multiple-hen cages: Comparison with control and commercial lines program and responses. Poultry Sci. 74 (Suppl. 1): 101 (Abstr.).

Muller, L.D., F.E. Robinson, P.R. Goerzen, and J.J.R. Feddes, 1996. The effects of increasing day length and/or light intensity at 20 wk of age on sexual maturity in female broiler breeders. Poultry Sci. 75 (Suppl. 1): 57 (Abstr.).

Naito, M., K. Nirasawa, and T. Oishi, 1990. Duration of egg formation in hens selected for increased rate of lay under 23 h and 24 h light-dark cycles. Br. Poult. Sci. 31: 371-375.

National Research Council, 1984. Nutrient Requirements of Poultry. 8th rev. ed. National Academy Press, Washington, DC.

Nesheim, M.C., R.E. Austic, and L.E. Card, 1979. Poultry Production, 12th ed. Lea & Febiger, Philadelphia.

Nestor, K.E., and K.I. Brown, 1972. Light intensity and reproduction of turkey hens. Poultry Sci. 51: 117-121.

Nicholas, J.E., E.W. Callenbach, and R.R. Murphy, 1944. Light intensity as a factor in the artificial illumination of pullets. Pennsylvania Agric. Exp. Sta. Bull. No. 462.

Oliver, M.M., B.B. Bohren, and V.L. Anderson, 1957. Heritability and selection efficiency of several measures of egg production. Poultry Sci. 36: 395-402.

Olson, D.M., and F. Hertelendy, 1981. Plasma levels of 13, 14-dihydro-15-keto prostaglandin $F_{2\alpha}$ in relation to oviposition in the domestic hen (*Gallus domesticus*). Biol. Reprod. 24: 496-504 .

Olson, D.M., K. Shimada, and R.J. Etches, 1986. Prostaglandin concentrations in peripheral plasma and ovarian and uterine plasma and tissue in relation to oviposition in hens. Biol. Reprod. 35:1140-1146.

Ostrander, C.E., R.K. Ringer, H.C. Zindel and C.N. Turner, 1960. The effect of various light intensities on egg production of Single Comb White Leghorn pullets. Quart. Bull. Michigan St. Univ. Agric. Exper. Sta. 43: 292-297.

Palmer, S.S., and J.M. Bahr, 1992. Follicle stimulating hormone increases serum oestradiol-17β concentrations, number of growing follicles and yolk deposition in aging hens (*Gallus domesticus*) with decreased egg production. Br. Poult. Sci. 33: 403-414.

Pearl, R., 1912. The mode of inheritance of fecundity in the domestic fowl. J. Exper. Zool. 13: 153-268.

Poggenpoel, D.G., and J.E. Erasmus, 1978. Long-term selection for increased egg production. Br. Poult. Sci. 19: 111-123.

Proudman, J.A., 1995. The biology of egg production and fertility. pp. 128-148 *in*: Proceedings of First International Symposium on the Artificial Insemination of Poultry. M.R. Bakst and G.J. Wishart, ed. Poultry Science Association, Savoy, IL.

Ralph, C., S. Binkley, S.E. MacBride, and D.C. Klein, 1975. Regulation of pineal rhythms in chickens: effects of blinding, constant light, constant dark and superior cervical ganglionectomy. Endocrinology 97: 1373-1378.

Redshaw, M.R., and B.K. Follet, 1972. The physiology of egg yolk production in the hen. pp. 35-49 *in:* Egg Formation and Production, Freeman, B.M., and P.E. Lake, ed. British Poultry Science Ltd., Edinburgh.

Reiter, R.J., 1980. The pineal and it's hormones in the control of reproduction in mammals. Endocr. Rev. 1: 109-131.

Roberts, J., and J.S. Carver, 1941. Electric light for egg production. Agric. Eng. 22: 357-360, 364.

Robinson, F.E., 1986. Ovarian steroidogenesis in the domestic fowl. Ph.D. Thesis, University of Guelph.

Robinson, F.E., 1993. A study of mortality, egg quality, and egg production in Alberta table egg production units. Alberta Agric. Res. Institute. Project # AARI90M227.

Robinson, F.E., H.L. Classen, and C. Riddell, 1988. Effect of photoperiod manipulation and feed restriction on plasma androstenedione concentration and selected organ weights in broiler chickens. Poultry Sci. 67(Suppl. 1): 145 (Abstr.).

Robinson, F.E., and R.J. Etches, 1986. Ovarian steroidogenesis during follicular maturation in the domestic fowl (*Gallus domesticus*). Biol. Reprod. 35: 1096-1105.

Robinson, F.E., R.T. Hardin, and A.R. Robblee, 1990. Reproductive senescence in domestic fowl: Effects on egg production, sequence length and inter-sequence pause length. Br. Poult. Sci. 31: 871-879.

Robinson, F.E., N.A. Robinson, and T.A. Scott, 1991. Reproductive performance, growth rate, and body composition of full-fed versus feed-restricted broiler breeder hens. Can. J. Anim. Sci. 71: 549-556.

Robinson, F.E., T.A. Wautier, R.T. Hardin, J.L. Wilson, M. Newcombe, and R.I. McKay, 1996. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 2. Egg-type hens. Can. J. Anim. Sci. 76: 283-288.

Robinson, F.E., J.L. Wilson, M.W. Yu, G.M. Fasenko, and R.T. Hardin, 1993. The relationship between body weight and reproductive efficiency in meat-type chickens. Poultry Sci. 72: 912-922.

Roland, D.A., M. Farmer, and D. Marple, 1985. Calcium and its relationship to excess feed consumption, body weight, egg size, fat deposition, shell quality, and fatty liver hemorrhagic syndrome. Poultry Sci. 64: 2341-2350.

Rowan, W., 1925. Relation of light to bird migration and developmental changes. Nature 115: 494-495.

Ruschkowski, S.R., and L.E. Hart, 1992. Ionic and endocrine characteristics of reproductive failure in calcium-deficient and vitamin D-deficient laying hens. Poultry Sci. 71: 1722-1732.

Saadeh, H.K., J.V. Craig, L.T. Smith, and S. Weardon, 1968. Effectiveness of alternative breeding systems for increasing rate of egg production in chickens. Poultry Sci. 47: 1057-1072.

Saito, N., K. Sato, and K. Shimada, 1987a. Prostaglandin levels in peripheral and follicular plasma, the isolated theca and granulosa layers of pre- and postovulatory follicles, and the myometrium and mucosa of the shell gland (uterus) during a mid-sequence oviposition cycle of the hen (*Gallus domesticus*). Biol. Reprod. 36: 89-96.

Saito, N., K. Shimada, and T.J. Koike, 1987b. Interrelationship between arginine vasotocin, prostaglandin, and uterine contractility in the control of oviposition in the hen (*Gallus domesticus*). Gen. Comp. Endoncrinol. 67: 342-347.

Schulman, N., M. Tuiskula-Haavisto, L. Siitonen, and E.A. Mantysaari, 1994. Genetic variation of residual feed consumption in a selected Finnish egg-layer population. Poultry Sci. 73: 1479-1484.

Shanawany, M.M., 1993. Ahemeral lighting and reproductive efficiency in breeding flocks. Wld's Poultry Sci. J. 49: 213-218.

Shanawany, M.M., T.R. Morris, and F. Pirchner, 1993a. Influence of sequence length on the response to ahemeral lighting late in lay. Br. Poult. Sci. 34: 873-880.

Shanawany, M.M., P. Sorensen, and F. Pirchner, 1993b. Genotypic differences in speed and magnitude of response to ahemeral lighting. Br. Poult. Sci. 34: 881-886.

Sharp, P.J., 1993. Photoperiodic control of reproduction in the domestic hen. Poultry Sci. 72: 897-905.

Shimada, K., I. Asai, M. Nishio, and T. Hattori, 1983. Ovarian prostaglandins (PGs) in the control of oviposition in the chicken. pp. 297-298 *in:* New Strategies for Improving Animal Production for Human Welfare, Proceedings of Fifth World Conference on Animal Production, Japanese Society of Zootechnical Science, Tokyo, Japan.

Shimada, K., and N. Saito, 1989. Control of oviposition in poultry. CRC Crit. Rev. Poultry Biol. 2: 235-253.

Simkiss, K., 1967. Calcium in Reproductive Physiology, Chapman & Hall, London.

Simpson, S.M., H.F. Urbanski, and J.E. Robinson, 1983. The pineal gland and the photoperiodic control of luteinizing hormone secretion in intact and castrated Japanese quail. J. Endocrinol. 99: 281-287.

Siopes, T.D., 1991a. Light intensity for turkey breeder hens: degree of darkness required during short-day light restriction and intensity threshold during photostimulation. Poultry Sci. 70: 1333-1338.

Siopes, T.D., 1991b. Light intensity effects on reproductive performance of turkey breeder hens. Poultry Sci. 70: 2049-2054.

Siopes, T.D., 1992. Effect of light intensity level during prelay light restriction on subsequent reproductive performance of turkey breeder hens. Poultry Sci. 71: 939-944.

Siopes, T.D., and H.A. Underwood, 1987. Pineal gland and ocular influence on turkey breeder hens. 1. Reproductive Performance. Poultry Sci. 66:521-527.

Siopes, T.D., and W.O. Wilson, 1974. Extraocular modification of photoreception in intact and pinealectomized coturnix. Poultry Sci. 53: 2035-2041.

Siopes, T.D., and W.O. Wilson, 1980. Participation of the eyes in the photostimulation of chickens. Poultry Sci. 59: 1122-1125.

Soares, J.H. Jr., 1984. Calcium metabolism and its control - a review. Poultry Sci. 63: 2075-2083.

Soller, M., T. Brody, Y. Eitan, T. Agursky, and C. Wexler, 1984. Minimum weight for onset of sexual maturity in chickens: Heritability and phenotypic and genetic correlations with early growth rate. Poultry Sci. 63: 2103-2113.

Solomon, , S.E., 1983. Oviduct. pp. 379-419 *in:* Physiology and Biochemistry of Fowl. Bell, D.J., and D.J. Freeman, ed. Academic Press, New York.

Somes, R.G., K.M. Cheng, D.E. Berman, and R.D. Crawford, 1990. Mutations and major variants of other body systems in chickens. pp. 273-292 *in:* Poultry Breeding and Genetics. R.D. Crawford, ed. Elsevier, Amsterdam.

Stabenfeldt, G.H., and L.E. Edqvist, 1984. Female reproductive processes. pp. 798-832 *in*: Duke's Physiology of Domestic Animals, 10th edition, Swanson, M.J., eds. Cornell University Press, New York, NY.

Summers, J.D., and S. Leeson, 1983. Factors influencing early egg size. Poultry Sci. 62: 1155-1159.

Taylor, T.G., 1965. Calcium-endocrine relationships in the laying hen. Proc. Nutr. Soc. 24: 49-54.

Taylor, T.G., 1972. The role of calcium in egg production. pp. 107-111 *in:* Egg Formation and Production, Freeman, B.M., and P.E. Lake, ed. British Poultry Science Ltd, Edinburgh.

Taylor. T.G., and F. Hertelendy, 1961. Changes in blood calcium associated with egg shell calcification in the domestic fowl. 1. Changes in the diffusible calcium. Poultry Sci. 40: 115-123.

Tilly, J.L., K.I. Kowalski, and A.L. Johnson, 1991. Stage of ovarian follicular development associated with the initiation of steroidogenic competence in avian granulosa cells. Biol. Reprod. 44: 305-314.

Tucker, S.A., and D.R. Charles, 1993. Light intensity, intermittent lighting and feeding regimen during rearing as affecting egg production and egg quality. Br. Poult. Sci. 34: 255-266.

van Krey, H.P., 1990. Reproductive biology in relation to breeding and genetics. pp. 61-90 *in:* Poultry Breeding and Genetics. R.D. Crawford, ed. Elsevier, Amsterdam.

van Middelkoop, J.H., 1971. Shell abnormalities due to the presence of two eggs in the shell gland. Arch. Geflügelkd. 35: 122-127.

van Middelkoop, J.H., 1972. The relationship between ovulation interval of White Plymouth Rock pullets and the laying of abnormal eggs. Arch. Geflügelkd. 36: 223-230.

van Tienhoven, A., 1981. Neuroendocrinology of avian reproduction, with special emphasis on the reproductive cycle of the fowl (*Gallus domesticus*). Wld's Poultry Sci. J. 37:156-176.

Waddington, D., M.M. Perry, A.B. Gilbert, and M.A. Hardie, 1985. Follicular growth and atresia in the ovaries of hens (*Gallus domesticus*) with diminished egg production rates. J. Reprod. Fertil. 74: 399-405.

Wautier, T.A., 1994. The effects of timing of photostimulation on the carcass composition and reproductive efficiency in commercial egg-type and meat-type female chickens. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Whetham, E.O., 1933. Factors modifying egg production with special reference to seasonal changes. J. Agric. Sci. 23: 383-418.

Williams, J.B., and P.J. Sharp, 1978. Ovarian morphology and rates of ovarian follicular development in laying broiler breeders and commercial egg producing hens. Br. Poult. Sci. 19: 387-395.

Wilson, S.C., and P.J. Sharp, 1976. Induction of luteinizing hormone release by gonadal steroids in the ovariectomized domestic hen. J. Endocrinol. 71:87-98.

Wilson, W.O., A.E. Woodard, and H. Abplanalp, 1956. The effect and after-effect of varied exposure to light on chicken development. Biol. Bull. 111: 415-422.

Wolfson, A., 1966. Environmental and neuroendocrine regulation of gonadal cycles and migratory behaviour in birds. Recent Progr. Hormone Res. 22: 177-244.

Wurtman, R.J., 1967. Effects of light and visual stimuli on endocrine function. pp. 19-59 *in:* Neuroendocrinology. Vol. 2. Martini, L., and W.F. Ganong, ed. Academic Press, NY.

Wurtman, R.J., 1974. The effects of light on man and other mammals. Ann. Rev. Physiol. 37: 467-482.

Yoo, B.H., B.L. Sheldon, and R.N. Podger, 1986. Analyses of oviposition times and intervals in a wide range of layer flocks under normal and continuous lighting regimes. Br. Poult. Sci. 27: 267-288.

Yu, M.W., F.E. Robinson, R.G. Charles, and R. Weingardt, 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. Poultry Sci. 71: 1750-1761.

Zakaria, A.H., H. Sakai, and K. Imai, 1984a. Time of follicular transformation to the rapid growth phase in relation to the ovulatory cycle of laying hens. Poultry Sci. 63: 1061-1063.

Zakaria, A.H., T. Miyaki, and K. Imai, 1984b. The relationship of clutch length and egg position on ovarian follicular growth in laying hens. Poultry Sci. 63: 1250-1254.

II. OVARIAN MORPHOLOGY, EGG PRODUCTION AND LAYING PROFILES IN TWO COMMERCIAL STRAINS OF EGG-TYPE HENS DIFFERING IN AGE AT SEXUAL MATURITY

II.1 INTRODUCTION

Modern strains of Single Comb White Leghorn (SCWL) chickens have been developed through intensive programs of genetic selection. Primary breeders have selected for improvement in such traits as age at sexual maturity, peak egg production, persistency of lay, feed efficiency, viability and disease resistance, egg weight and size, albumen and shell quality, fertility, hatchability, and the incidence of meat or blood spots in eggs. The evidence of genetic progress in egg-type chickens is well known and has been previously reported (Fairfull and Gowe, 1990; Hunton, 1990).

Management practices have also evolved as knowledge has increased. Exposing chickens to increasing day-lengths is known to advance sexual maturation and stimulate higher rates of lay (Morris, 1994). Photoschedule manipulation has become a standard industry procedure to influence flock age at onset of lay, rate of egg production, egg size, and feed efficiency (Etches, 1996). It is known that stimulating sexual maturity by photostimulation at too young an age causes increased production of smaller eggs in both turkeys (Siopes, 1992) and egg-type chickens (Kling *et al.*, 1985; Robinson *et al.* 1996b), as well as poorer persistency of lay in White Leghorn hens (Harrison *et al.*, 1969). Siopes (1992) reported an inverse relationship between age at lighting and time required to initiate egg production in turkeys. Robinson *et al.* (1996a; 1996b) reported a decrease in duration between photostimulation and sexual maturity with increasing age of photostimulation in broiler breeder and SCWL hens. Initial egg weight was not affected in these studies. Egg production was higher for the SCWL pullets photostimulated at 16 wk (+ 6.2 eggs), although it was less than expected considering initiation of lay was 13.7 d earlier than the pullets photostimulated at 20 wk (Robinson *et al.*, 1996b). The difference from expected results was shown to result from longer laying sequences in the pullets photostimulated at 20 wk (Robinson *et al.*, 1996b).

Egg production in domestic fowl occurs in sequences which have been defined as any number of consecutive days upon which an oviposition occurs terminated by one or more pauses of non-laying days (Fraps, 1955; Etches, 1984). Sequence length profile analysis of broiler breeder hens has shown that hens lay short sequences of 6 to 10 d shortly after the onset of production, with one long or "prime" sequence being laid 6 to 8 wk after that time (Robinson *et al.*, 1990). Peak flock egg production coincided with prime sequence in a majority of hens and the decline observed in egg production with advancing age was caused in part by a decline in sequence length and an increase in inter-sequence pause length.

There is an optimum number of large yellow follicles (LYF) required to maintain a high rate of lay. Zakaria *et al.* (1984) concluded that inter-sequence pauses could either be caused by failure of a follicle to be recruited into the rapid growth phase or by failure of the hen to ovulate. It has been clearly shown that excess energy intake in broiler breeder hens can produce an overabundance of follicles on the ovary, and results in a loss of reproductive control (Hocking *et al.*, 1987, 1989; Robinson *et al.*, 1991, 1993). This is evidenced by increased incidence of erratic oviposition, multiple-yolked eggs, shell deformities, internal ovulation and internal oviposition (van Middelkoop, 1972; Yu *et al.*, 1992). A high rate of lay can not be supported by insufficient quantity of LYF (Zakaria *et al.*, 1984) and it is generally accepted that 6-8 LYF are normal for high producing egg laying strains (Gilbert, 1971; Williams and Sharp, 1978). The absence of a mature follicle on the ovary may result from a hen's failure to recruit into the hierarchy of large yellow follicles (Williams and Sharp, 1978), atresia (Gilbert *et al.*, 1983; Waddington *et al*, 1985), or factors such as disease which can inhibit follicular growth and development.

Pauses are a regular occurrence even when a mature follicle is ready to ovulate. Etches and Schoch (1984) reported that successive ovipositions of a sequence occur later each day and intra-sequence oviposition interval is often greater than 24 h. In mid-sequence, ovulation follows oviposition by about 30 min (Warren and Scott, 1935; Melek *et al.*, 1973) and is associated with a pre-ovulatory LH surge. As time of oviposition advances, the pre-

ovulatory LH surge does not occur if it exceeds the "open period" for LH release (Etches, 1990). The hen fails to ovulate the mature or F1 follicle which results in a pause on the following day. Factors that prolong follicular development or egg formation may therefore cause increased intra-sequence oviposition interval and effectively shorten sequences.

The obvious evidence of the hen's ovulatory cycle is the ovipository cycle, and these two cycles are displaced by the time of egg formation in the oviduct (Fraps, 1955). Etches and Schoch (1984) found agreement between the time of oviposition predicted by a mathematical model of the ovulatory cycle and the observed times of oviposition under 21, 24 and 28 h photoschedules. It is also known that secondary factors such as noise, temperature and feeding activity are known to shift time of oviposition (Cain and Wilson, 1974; Bhatti and Morris, 1977). Yoo *et al.* (1986) found the rate of lay to 301 d of age under a 14L:10D photoperiod increased linearly by 6.3% for each hour decrease in mean intra-sequence oviposition interval, with a limit at about 24 h. These authors concluded that the observed reduction of oviposition interval was a result of more than one physiological change. A reduction in oviposition intervals which were longer than 24.5 h was likely caused by a reduction of the time spent in the oviduct by an egg, with little change in mean ovulation time. A reduction in oviposition intervals shorter than 24.5 h was likely a result of increased follicular maturation rates and therefore resulted in advancement of ovulation time (Yoo *et al.*, 1986). Further support for a model which includes egg formation time in the oviduct may be provided by Gow *et al.* (1985). These authors reported a reduction of 1.3 h in time interval between the pre-ovulatory LH surge and the oviposition of the resulting ovulation in a line of Australorp hens selected for shortened intra-sequence oviposition interval. Selection had no significant effect on the interval between oviposition and the following LH peak in either Australorp or White Leghorn breeds. Melek *et al.* (1973) concluded that White Leghorns of the 1970s had essentially the same time relationship between oviposition and the following ovulation (30 min) as White Leghorn hens of the 1930s. McClung *et al.* (1976) found no significant increase in annual egg production under selection for shorter intra-sequence interval

because the resulting longer sequences were offset by longer inter-sequence pauses. Gow *et al.* (1985) observed that selection for reduced intra-sequence oviposition interval increased partial-record egg production (29 - 33 wk of age) and was associated with increased sequence length.

Bohren *et al.* (1981) have previously reported a consistent increase in number of eggs to 40 wk of age resulting from selection for early sexual maturity, although there was no consistent increase in annual number of eggs produced. There was also no correlated response observed in percent production to 40 wk or annual percent production. These data demonstrate that gains in early egg numbers from earlier sexual maturity do not necessarily contribute to increased total egg production or production rate. Robinson *et al.* (1990) reported that length of the prime sequence was correlated with total egg output ($r = 0.3992$). Robinson *et al.* (1996b) has reported that prime sequence length was numerically greatest in SCWL hens photostimulated at 20 wk compared to 16 and 18 wk.

Selection pressure to improve feed efficiency in SCWL has resulted in decreased mature BW (Hunton, 1990). Earlier sexual maturity is known to reduce egg size (Harrison *et al.*, 1969; Bell *et al.*, 1982), partly as a result of decreased BW at sexual maturity (Summers and Leeson, 1983). Pullets of strains which have been genetically selected to begin egg production at lower age and BW may exhibit decreased persistency of lay similar to hens photostimulated at an early age (Harrison *et al.*, 1969). Limited data is available examining strain differences in age at sexual maturity, carcass characteristics, ovarian morphology and egg production profiles for SCWL. The objective of this research was to compare carcass and reproductive morphometrics, egg production and laying patterns between two strains of SCWL believed to be genetically different for age at sexual maturity. The relationship of production profiles with ovarian morphology and carcass characteristics at sexual maturity and end of lay were also examined. Although both selected experimental strains were chosen according to their expected age of first oviposition, no scientific data was available to confirm these differences in modern commercial strains of SCWL.

II.2 MATERIALS AND METHODS

II.2.1 Stocks and Diet

A total of 600 Single Comb White Leghorn (SCWL) pullets of two commercial strains [early maturing Babcock[1] B300 (EM) and later maturing Shaver[2] White (LM)], were reared to 17 wk of age. The rations provided to the birds was as follows: Chick starter from 0 to 6 wk; Grower 1 from 6 to 12 wk; Grower 2 from 12 to 16 wk; Pre-layer from 16 to 20 wk; Layer ration from 20 wk to end of lay. The nutrient analysis of each ration is listed in Table II-1. Feed was provided *ad libitum*, while clean drinking water was available at all times.

II.2.2 Management and Experimental Design

Pullets of each strain were reared in floor pens (4.75 x 5.85 m) of 150 birds each in a light-tight facility. Chicks were initially subjected to 23L:1D photoschedule which was reduced to 17L:7D at 1 wk and 14L:10D at 2 wk. At 3 wk of age, the photoschedule was reduced to 10L:14D and light was maintained on that schedule until 18 wk. Beak trimming and dubbing were performed at 7 d of age. Each pullet was wing-banded at 6 wk and individually weighed at 6, 9, 12 and 16 wk. At 16 wk, the 150 pullets of each strain closest to the strain's mean BW were selected and randomly assigned to one of nine experimental groups. Seventy pullets of each strain were assigned to A-group and were designated be killed at specific time intervals during sexual maturation. The A-group was further subdivided into seven equal groups (A-17 to A-23) corresponding with the scheduled age (17 - 23 wk) when they would be killed. Twenty pullets of each strain were assigned to be killed on the day following first oviposition and were designated as the B-group. The remaining 60 hens of each strain were designated as C-group and housed until 68 wk. At 17 wk of age, pullets for each group were moved to individual laying cages in an alternating, stratified design by strain.

Pullets were moved to individual laying cages at 17 wk of age and were

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[1] ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851.

[2] Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

photostimulated at 18 wk with a one hour increase in daylength to 11L:13D. A photophase increase of 15 min was supplied on subsequent weeks until 14L:10D was achieved at 30 wk of age. Birds were then maintained on the 14L:10D photoschedule throughout lay until 68 wk of age. Indications of cage-layer fatigue became apparent at 35 wk and symptoms were alleviated by supplying supplemental oyster shell to all birds in the feed troughs on a weekly basis. Hens were culled if they ceased to eat, drink and produce eggs, and their carcasses were submitted to the Veterinary Pathology Laboratory of Alberta Agriculture, Food and Rural Development, Edmonton for post-mortem examination.

Surviving birds were weighed at weekly intervals from 17 to 26 wk and at bi-weekly intervals from 26 to 68 wk of age. On the afternoon (1-3 pm) of the previous day to being killed, a 10 ml blood sample was collected from each bird by brachial venipuncture. The bird was weighed and then subjected to feed withdrawal overnight (12-20 h) to permit gut clearance. All experimental procedures performed on live birds were within the principles and guidelines approved by the University of Alberta, Faculty of Agriculture, Forestry and Home Economics, Animal Policy and Welfare Committee.

II.2.3 Carcass Examination

Each pullet was killed by cervical dislocation and the intact carcass was weighed. The left shank length was recorded (length of the tibiotarsus from the top of the hock joint to middle of the footpad) as an indicator of frame size. The weights of the abdominal fat pad including the fat surrounding the gizzard, breast muscle (*pectoralis major* and *minor*), liver, oviduct, ovary and stroma were recorded. The stroma weight was comprised of the ovarian tissue remaining after the LYF (greater than 10 mm diameter) were removed. Carcass component weights were expressed both by absolute organ weight basis and as a percentage of BW at processing. The LYF were counted and individually weighed. The number of small yellow follicles (SYF; 5 - 10 mm diameter) and post-ovulatory follicles were recorded. The birds were inspected for traits indicating their state of reproductive health, such as the

incidence of internal ovulation, internal oviposition, ovarian regression, and follicular atresia.

All carcass components, except the liver, were labelled and stored together at -20°C. Each liver was labelled and individually stored at -20°C for subsequent analysis of total liver lipid content. Individual whole body composition was determined for each bird following the procedure described by Yu *et al.* (1990). Each carcass was autoclaved for 3.5 h and homogenized using an industrial pressure-cooker and blender. A 500 ml subsample of each homogenized carcass was freeze-dried and subjected to proximate analysis in duplicate for dry matter, ash, crude protein, and petroleum ether-extractable lipid content (Association of Official Analytical Chemists, 1980). The livers were freeze-dried and ground in a household blender. Total lipid content was determined by petroleum ether extraction. For each tissue analysis, a 2% difference between duplicates was accepted, with the exception of a 5% difference allowable for carcass ash content duplicates. Re-analysis was performed on carcass samples not meeting these criteria. In a few cases where sufficient liver tissue was unavailable for re-analysis in duplicate, a third subsample was analyzed and the two results with the least difference were averaged.

Blood samples were centrifuged at 2500 RPM for 11 minutes at 4° C and the plasma portion was stored at -20° C in individually labelled vials. Plasma estradiol-17β concentration was determined on blood samples from A-17, A-18, A-19, A-20, and B-group pullets using an antibody-coated tube, competitive-binding RIA[3]. Estradiol-17β concentrations in different volumes of a plasma sample were measured to determine parallelism (vol: mean ± SEM; 50μl: 31 ± 3.0 pg/ml; 100μl: 101.8 ± 6.8 pg/ml; 200μl: 247.6 ± 8.4 pg/ml; 400μl: 599.5 ± 14.0 pg/ml). Duplicate 200 μl samples of plasma were assayed with the controls indicating an intra-assay coefficient of variation of 8.35% and an inter-assay coefficient of variation of 4.09%. The detection limit of the RIA was approximately 8 pg/ml and the antiserum was highly specific for estradiol-17β as stated by the manufacturer. With the exception of estrone (10.0%), *d*-Equilenin (4.4%), estrone-β-D-glucuronide (1.8%) and ethinyl estradiol-17β

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[3]Kit Number TKE25, Diagnostic Products Corp., Los Angeles, CA 90045-5597

(1.8%), all other naturally occurring steroids or therapeutic drugs tested had a cross reactivity less than 1%. Duplicate 1.5 ml samples of plasma were sonicated prior to analysis of quantitative lipid content by chloroform-methanol method.

II.2.4 Egg Production

Individual daily egg production records were kept for C-group birds until 68 wk. The incidence of abnormal eggs (soft-shelled, shell-less, double yolked, broken, abnormal or pecked) was recorded as an indication of shell quality. At 68 wk of age, the C-group hens were killed and analyzed for carcass traits and ovary morphology as previously described. Egg weights were recorded daily from 17 to 24 wk of age and once per week thereafter.

Egg production data were based on survivors and eliminated 10 hens per strain. Survivors were defined according to McMillan *et al.* (1990) as the hens that had laid at a minimum rate of 20% in each third of the laying period, and survived to the end of the test to 476 d of age. Average hen-day production for each strain was calculated in two different ways, relative to both photostimulation and first oviposition. The first method was calculated from the total eggs produced by each hen divided by the number of days from photostimulation to 68 wk; the second method divided the total number of eggs for each hen by the number of days from first oviposition to 68 wk. Hen-day production was calculated for each 4 wk period from 17 wk of age to the end of the trial.

Sequence length, inter-sequence pause length, and sequence profiles were determined from oviposition records using similar procedures as Robinson *et al.* (1990), which has been derived from the methods of Blake and Ringer (1987). Sequence length was measured by counting the number of days on which an egg was laid before a non-laying or pause day. In the event that two eggs were laid on the same day, one egg was recorded as the previous days egg only if a) there was no egg laid the previous day, and b) one of the two eggs was laid prior to the first morning collection when the lights came on. A sequence length number for each day was calculated for every hen based on the sequence length that each hen was laying

at that time. For example, a hen laying a 7 d sequence was assigned a seven on each of those egg-laying days. The sequence length profiles were constructed by averaging the daily sequence length numbers for each week. The prime sequence was measured as the longest uninterrupted laying sequence around the time of peak production (Robinson *et al.*, 1990). The number and length of each sequence was recorded and averaged into the mean sequence length for each hen.

II.2.5 Statistical Analysis

A one-way analysis of variance was used to evaluate strain (s = 2) differences for each time period group, using the General Linear Models (GLM) procedure of SAS® software (SAS Institute, 1992). Differences in egg production curves from first oviposition to 68 wk of age were determined by Kolmogorov-Smirnov Test. Pearson correlation coefficients were computed between BW at various ages, egg production parameters and carcass examination traits at 68 wk within each strain and on an entire flock basis. The error variation was considered to be birds within strain, and all statements of significance were assessed at $P < 0.05$. Data from C-group hens were also sorted into the upper and lower 50%, and upper and lower 25% by total eggs produced, prime sequence length and age at first oviposition for the total flock, regardless of strain, and these data are included in Appendix A. Regression equations for hen-day egg production and carcass trait development have been provided in Appendix B.

II.3 RESULTS AND DISCUSSION

II.3.1 Age at Sexual Maturity

The age at first oviposition differed significantly between strains as indicated by B-group pullets. The average age of first oviposition was 137.5 d for the EM strain and 142.1 d for the LM strain (Table II-2). Considering that all pullets were photostimulated at 126 d of age, the 4.6 d difference in age of sexual maturity represents a 28.6 % shorter duration

between photostimulation and first oviposition in the EM strain than the LM strain. These data demonstrate that differences exist between strains of SCWL for age at sexual maturity. While earlier sexual maturity under a similar photoschedule may represent a shorter response time to lighting, it is also likely to include genetic factors as some strains selected for early maturity may begin sexual development prior to photostimulation.

II.3.2 Carcass Examination

Body weight of the A-group pullets was similar between strains for 17, 18, 20, 21, and 23 wk (Table II-3). Body weight was heavier in the EM strain at 19 wk, and lighter at 22 wk compared to the LM strain. The B-birds of the EM strain killed at first oviposition were lower in BW than their LM counterparts (EM: 1405 g; LM: 1456 g; Table II-2). Considering the similarity of BW throughout development, this difference in BW at first oviposition was likely related to earlier sexual maturity in the EM pullets. Group-C hens demonstrated that the LM strain continued to increase in BW after sexual maturity and were consistently heavier than the EM strain to 68 wk. (Figure II-I). Shank length was not different for any time period.

Breast muscle weight (absolute basis) of the A-group birds was significantly different between strains at 19 and 22 wk of age (Table II-4). Breast muscle weight expressed relative to BW was lower in the EM strain only at 17 and 21 wk. Oviduct weight (absolute basis) was higher in the EM strain at 19, 21, and 22 wk (Table II-5). Oviduct weight expressed as a percent of BW was significantly higher in the EM strain for 18, 19, 21, and 22 wk of age. Examination of the pullets killed at sexual maturity (B-group) revealed that breast muscle weight was lower and oviduct weight was higher in the EM strain than in the LM strain, expressed both in absolute and relative terms (Table II-2). At 68 wk of age, oviduct weight was still greatest and breast muscle weight was still lowest in the EM strain, both on an absolute basis and expressed as a percentage of BW (Table II-6). These results may suggest a preferential allocation of protein by the EM hens toward lean tissue for reproductive function

(oviduct) instead of skeletal muscle.

Abdominal fat pad weight (absolute basis) was heavier in the EM than the LM strain at 18, 19 and 23 wk of age (Table II-7). When expressed relative to BW, EM pullets had heavier fat pads than LM only at 18 and 23 wk. Although fat pad weight at sexual maturity did not differ between strains (Table II-2), fat pad weight was significantly heavier in the LM strain at 68 wk (Table II-6). The heavier fat pads in the LM strain at 68 wk is consistent with their heavier BW throughout the laying period.

Liver weight did not differ between strains from 18 through 22 wk of age, either in absolute or relative terms, although heavier livers were found in the EM strain at 23 wk of age (Table II-8). The dry weight of liver was heavier in the EM strain at 18 and 23 wk compared to the LM strain. Absolute, relative and dry liver weight did not differ between strains at sexual maturity (Table II-2), however liver weight on an absolute basis was lighter in the EM strain at 68 wk of age (C-group) than in the LM strain (Table II-6).

Ovary weight was higher in the EM strain at 17, 19, 21 and 22 wk of age, both on an absolute basis and relative to BW (Table II-9). The weight of the stroma was significantly heavier in the EM strain for all periods from 17 through 23 wk of age (Table II-10). Total LYF weight was heavier in the EM strain at 19, 21 and 22 wk (Table II-11). The absolute weight of total LYF, ovary and stroma did not differ between strains when killed at first oviposition (Table II-2) or at 68 wk of age (Table II-6), but relative ovary weight was heavier in EM than LM at end of lay. The EM strain had a greater number of SYF and LYF on 19, 21, 22 and 23 wk (Table II-11). Since ovary weight tended to increase with number of LYF, this explains the presence of greater ovary weights generally found in the EM strain. There was no difference in the number of SYF (EM: 5.0; LM: 5.2), LYF (EM: 7.0; LM: 6.4) or POF (EM: 2.4; LM: 2.5) between strains at sexual maturity (Table II-2). Although there was also no difference in number of LYF (EM: 5.2; LM: 5.3) between strains at 68 wk, the LM strain had a higher number of SYF at that time (EM: 11.5; LM: 14.5; Table II-6).

The carcass examination and reproductive characteristics observed in the A and B-

group birds during the period of 17 to 23 wk of age were generally indicative of earlier onset of sexual maturation in the EM than the LM strain. Figures II-2 illustrate the general increased growth of reproductive parameters (oviduct weight, ovary weight, stroma weight, LYF weight and the quantities of SYF and LYF) expected as pullets become sexually mature. It also consistently demonstrates the earlier response in the measured traits for the EM strain compared to the LM strain.

Following photostimulation at 18 wk, there was a rapid increase in the concentration of plasma estradiol-17β as sexual development was initiated (Table II-12). The EM and LM pullets demonstrated plasma estradiol-17β concentration increases of 36.6% and 62.1%, respectively, between 18 and 19 wk of age, although there was no difference between strains for 17 through 20 wk of age. Plasma lipid concentration was also observed to increase following photostimulation, with an increase evident in the EM pullets at a younger age than LM (Table II-12). Plasma lipid concentration was higher in the EM strain for 18, 19 and 20 wk of age. It is interesting to note that the increased level of plasma lipid in the EM strain at 18 wk suggests increased lipogenesis for ovary development may have begun prior to photostimulation. Early sexual development in the EM strain is also evident from the increased liver lipid content observed prior to photostimulation at 18 wk of age (Table II-13). Liver lipid content was significantly higher in the EM strain for both 17 and 18 wk, calculated as lipid weight and as a percent of liver DM, but were similar for both strains from 19 to 23 wk of age and at sexual maturity (Table II-2).

There was no difference between strains for carcass moisture content, expressed either as weight (Table II-14) or as a percentage of the carcass (Table II-15), for any A-group pullets. The EM strain had a lower carcass protein content on a percentage basis on wk 23 (Table II-15). The LM strain had a higher carcass ash content (weight basis) at 19 wk of age (Table II-14). At 18, 19 and 23 wk of age the EM pullets had a higher carcass lipid weight and percent lipid content than the LM strain (Table II-14). This coincides with the same time periods in which significant differences were observed in abdominal fat pad weights between

the two strains. In comparing the results of proximate analysis for carcass composition, it can be seen that lipid generally replaced water as a percentage of the bird's body during maturation from wk 17 to 23 (Table II-15). The moisture content decreased by nearly 10% of the total carcass and coincided with a carcass lipid content increase of approximately 11-12%. There was no difference in protein or lipid content between the two strains in the B-group birds (Table II-16). However, the percentage of carcass ash was higher and the absolute weight of carcass moisture was lower in the EM strain than the LM strain at first oviposition.

Brody *et al.* (1980, 1984) and Soller *et al.* (1984) have reported the importance of threshold BW for the onset of sexual maturity. Since the reduced age at first oviposition in the EM strain was also associated with lower BW, either BW must not have been a limiting factor in achievement of sexual maturity, or selection has effectively altered the threshold limit. However, abdominal fat pad weight and total carcass lipid content were not significantly different between strains at sexual maturity. This would appear to support a minimum fat requirement for sexual maturity as previously reported by Bornstein *et al.* (1984). Robinson *et al.* (1996a,b) found no significant differences in carcass composition in broiler breeder pullets photostimulated in order to reach sexual maturity at different ages, and although there were differences in SCWL pullets, greatest increases in fat content were found in the early photostimulated pullets. Similar to Robinson *et al.* (1996b), the results of the present experiment support the hypothesis that a minimum fat content may be required for the onset of sexual maturity, and this value is likely to be near 15% carcass lipid content in SCWL.

The differences observed in levels of plasma estradiol-17β concentration, plasma and liver lipid concentration and the existence of LYF in some birds prior to photostimulation illustrated that these strains of SCWL do not require photostimulatory increases in daylength to initiate sexual maturity. This supports the finding of Eitan and Soller (1991), who have reported that although supplemental light had a significant effect on weight and age at first egg, it was not required for the onset of sexual maturity. Lupicki (1994) found that SCWL

(Shaver Starcross 288[4]) pullets housed under a 8L:16D photoperiod initiated lay in the absence of a photostimulatory increase in daylength, although first oviposition occurred at 158.7 d of age compared to 152.7 d for birds that were photostimulated at 20 wk of age. Robinson *et al.* (1996b) reported that although delaying photostimulation will delay the onset of lay in SCWL (Shaver Starcross 288), evidence of ovary and oviduct development could be seen prior to late photostimulation and response time to photostimulation was shortened as age increased. The plasma and liver lipid concentration data presented here provide further evidence of the EM strain pullets increasing lipogenesis for egg yolk formation at an earlier age than the LM strain, even prior to photostimulation at 18 wk of age.

The carcass traits at 68 wk of age indicate that the EM strain had allocated a greater percentage of nutrients and energy toward reproductive function than LM strain hens. BW was significantly lower in the EM strain throughout lay (Table II-2). Oviduct and ovary weight expressed relative to BW were significantly higher at 68 wk in the EM strain, while breast muscle and fat pad weight were higher in the LM strain. The increased fat pad weight in the LM strain indicates that either a lower percentage of energy intake was required for growth and production, or that feed intake was higher in the LM strain relative to requirements.

At 35 wk of age, symptoms of cage-layer fatigue became apparent and were alleviated by the addition of supplemental oyster shell in the feed troughs on a weekly basis. This is consistent with the results obtained by Keshavarz and Nakajima, (1993), who reported oyster shell was effective in improving shell quality even when diet contained plentiful calcium. Although feed intake was not recorded in this experiment, it is suggested that the lower weight EM strain consumed less feed and thereby less calcium. Mortality was restricted primarily to the EM strain beginning at 35 wk and laboratory analysis confirmed that the cause of early cessation of lay and illness were the result of osteoporosis / osteomalacia. By 68 wk of age, the overall mortality was 15.8 % and was similar between strains (EM, 10; LM, 9). Mortality

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[4] Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

toward the end of lay was primarily in LM strain hens and laboratory analysis of these hens indicated a high incidence of fatty liver haemorrhagic syndrome. The incidence of mortality was high in comparison to the average values of 6.06% reported by Robinson (1993) for commercial flocks in Alberta, although the causes of mortality were consistent with those found for other flocks. The results presented here suggest that the EM strain may be predisposed to metabolic disease caused by nutrient deficiency (ie: calcium) while the heavier LM strain may have problems toward end of lay with obesity and fatty liver disease.

II.3.3 Egg production traits

Each of the two strains used in this study performed well in relation to breeder's targets (Anonymous, 1991, 1993). Total egg production was similar for the two strains of SCWL during the 350 days after photostimulation, with the EM and LM strains producing an average of 296.5 and 298.3 eggs respectively (Table II-17). Average hen-day production relative to photostimulation was similar for both strains (EM, 84.7 %; LM, 85.4 %). When the difference in age at first oviposition was considered, the LM strain produced an average of 90.4 % of hen-days, while the EM strain produced an average of 88.2 %.

Although total egg production was similar between the two strains, there were significant differences in laying profiles. The LM strain had an increased ability to maintain production of one egg per day as evidenced by the longer prime and average sequence lengths. The prime egg-laying sequence was 18.8 d longer in the LM strain compared to the EM strain (EM: 52.6 d; LM: 71.4 d; Table II-17). The prime sequence lengths observed for both SCWL strains in this experiment were similar to those previously reported for SCWL hens (68.7, 81.7, and 82.4 d) when they were photostimulated at 16, 18 and 20 wk of age respectively (Robinson *et al.*, 1996b), and are considerably longer than the average prime sequence length (24.3 d) for broiler breeder hens (Robinson *et al.*,1990). Figure II-3 illustrates the profiles of sequence length over the laying period and demonstrates the increased ability of the LM hens to maintain laying one egg per day for a significantly longer period of time than

the EM hens. The average sequence length of the EM strain was 8.7 d compared to 12.8 d in the LM strain (Table II-17). The increased number of shorter sequences in the EM strain, with no difference in inter-sequence pause length. contributed to similar total egg production as observed from the LM strain. Figure II-4 illustrates the histogram of hens grouped by the length of their prime egg laying sequence, and reveals that 8% of the LM strain hens had prime sequences longer than 140 d, which no EM strain hen achieved. As well, 42% of the EM hens had a prime sequence shorter than 40 d compared to only 28% of the LM strain. Although no differences were observed in inter-sequence pause length between strains, pause lengths at sexual maturity were initially high (2 - 5 d) and rapidly decreasing to one day in length for most of the laying period (unpublished data). Similar to the results of Robinson *et al.* (1990) with broiler breeder hens, inter-sequence pause length increased toward the end of lay (56 wk). The decline in the hen-day production as the laying period progresses can be attributed to both a decrease in sequence length and an increase in inter-sequence pause length. Further studies should be conducted to accurately record the time of each daily oviposition to determine the degree by which intra-sequence oviposition intervals increase as the laying cycle progresses and their relationship to shortening sequence lengths.

Considering the difference in BW between strains, it was surprising that neither first nor last egg weight (Table II-17) were different between strains. The hen-day egg production curves (Figure II-5a) were also not different between strains. When the egg weight, hen-day egg production, and weekly egg mass curves (Figure II-5) are compared, it becomes apparent that weekly egg mass output remained relatively constant to 68 wk of age. This is primarily a result of the decline in hen-day egg production coinciding with increasing average egg weight.

Although total egg production was similar between strains, the production of normal shelled eggs was greater in the LM strain hens (EM: 284.8; LM: 294.6; Table II-17). This was a result of the higher incidence of soft-shelled, shell-less, and double-yolked eggs produced by the EM strain (Table II-17). Yu et al. (1992) demonstrated the erratic oviposition and defective egg syndrome (EODES) is related to an excess number of LYF in

broiler breeder hens. In this study, the EM strain had a higher number of LYF for wk 19, 21, 22 and 23, although no difference was found at sexual maturity. These data would suggest that similar problems as found in over-weight broiler breeder hens may occur in egg-type hens which allocate high proportions of energy toward follicular development at an early age.

II.3.4 Correlation coefficients

In general, BW at various ages between 6 and 66 wk of age were correlated, with the exception of 17 and 18 wk BW to 66 wk BW (Table II-18). On a flock basis, BW at 18 wk of age (photostimulation) was highly correlated with BW at both 17 wk ($r = 0.862$) and 19 wk ($r = 0.882$). Correlations between 18 wk BW remained significant with BW to 58 wk of age, although the correlations generally decreased with age (26 wk, $r = 0.356$; 58 wk, $r = 0.214$).

On a flock basis, age at first oviposition was negatively correlated with BW at 18 wk of age ($r = -0.503$; Table II-19). These data are consistent with previous observations by Brody *et al.* (1984) that chickens of the same age which had started to lay were significantly heavier than those not laying. On a flock basis, BW at 18 wk was also correlated with the incidence of both double-yolked ($r = 0.217$) and abnormal shelled eggs ($r = 0.230$). For individual strains, 18 wk BW was correlated with soft-shelled eggs in the LM strain ($r = 0.282$; Table II-20) and abnormal shelled eggs in the EM strain ($r = 0.319$; Table II-21). Age at first oviposition was positively correlated with first egg weight on a flock basis ($r = 0.269$) and in each individual strain (LM, $r = 0.343$; EM, $r = 0.396$) as presented in Tables II-19, II-20, and II-21, respectively. First egg weight was not correlated with 18 wk BW in either strain or on a flock basis. On a flock basis, age of first oviposition was negatively correlated with the incidence of double-yolked ($r = -0.420$) and abnormal shelled eggs ($r = -0.244$; Table II-19). When each strain was analyzed independently, fewer correlations with defective egg types were observed in the LM strain (Table II-20) because of the significantly lower production of defective eggs by these hens (Table II-17).

On a flock basis there was a strong negative correlation between number of laying

sequences and both total eggs (r = -0.772) and normal eggs produced (r = -0.859; Table II-19). The production of normal eggs was negatively correlated with the production of defective eggs of various types: soft-shelled (r = -0.624), shell-less (r = -0.405), double-yolked (r = -0.197), and abnormal shelled eggs (r = -0.442). Normal egg production was positively correlated with total egg production (r = 0.851), prime sequence length (r = 0.537) and average sequence length (r = 0.682). Prime sequence length also showed a strong positive correlation with total egg production (r = 0.530) and average sequence length (r = 0.688), but was negatively correlated with 18 wk BW (r = -0.218), quantity of soft-shelled eggs (r = -0.211), and number of sequences (r = -0.680). On a flock basis, the production of defective egg types, (soft-shelled, shell-less, double-yolked, and abnormal shelled) were positively correlated with each other (Table II-19), with the exception that the correlation between double-yolked and soft-shelled eggs did not reach significance at the 0.05 level (p = 0.063). The greatest correlation among defective eggs was between soft-shelled and abnormally shelled eggs (r = 0.536) on a flock basis (Table II-19).

The weights of breast muscle, abdominal fat pad, and liver at 68 wk of age were strongly correlated with BW at 66 wk of age and with each other (Table II-22). Oviduct weight at 68 wk was only correlated with egg weight at 68 wk of age. Egg weight at 68 wk of age was positively correlated with BW at 66 wk of age (r = 0.252), oviduct weight (r = 0.307), and ovary weight (0.329), but was negatively correlated with total egg production (r = -0.394) and average sequence length (r = -0.284). The number of LYF on the ovary at 68 wk was positively correlated with ovary weight (r = 0.319) and prime sequence length (r = 0.209), although number of SYF was not correlated with any parameter measured. Total egg production was not significantly correlated with any of the organ weights at 68 wk or with the number of large or small yellow follicles.

A strong correlation was observed between prime sequence length and total egg output on a flock basis (r = 0.530; Table II-19) and for each strain (LM, r = 0.578; EM, r = 0.460; Tables II-20, 21). These values are larger than the correlation values between prime sequence

length and total egg output previously reported (r = 0.399) by Robinson *et al.* (1990). These authors concluded that there was neither any evidence to suggest that hens laying extremely long prime sequences exhibited lower rates of egg production later in lay, nor that hens with short prime sequences compensated with higher egg production later.

Robinson *et al.* (1996b) provided evidence that delaying sexual maturity in SCWL by later photostimulation resulted in fewer but longer sequences. These authors concluded that the earlier photostimulated pullets may not have had the body reserves necessary to reach peak egg production, and the reserves they did possess may have been depleted by this time. The results obtained in the present study indicate that genetic selection for earlier sexual maturity, feed efficiency or lower BW may compromise egg production in a similar manner.

There are a number of possible explanations for the differences in quantity and length of sequences between strains. 1) The difference could result from heavier selection by the primary breeder for peak egg production traits in the development of the LM strain. 2) The earlier maturing strain may have compromised control of follicular recruitment. Since the EM strain appeared to have a greater allocation of energy toward the ovary at a younger age, the possibility exists that this caused an impairment in ovarian control similar to that occurring in *ad-libitum* fed broiler breeder hens (Robinson *et al.*, 1993). This explanation would appear to be supported by the increased incidence of double-yolk eggs, which had a negative correlation (r = -0.420) with age at sexual maturity, and is typical of EODES. 3) Considering that the EM strain had lower BW, feed intake may have been lower and therefore insufficient energy could have been consumed to maintain a maximal rate of follicular development. A mature follicle would then have been unavailable on a specific day during the "open period" for LH release. Limited body reserves would have been depleted by the time of peak egg production as suggested for the early induced pullets discussed previously by Robinson *et al.* (1996b) This explanation would be supported by the observation of decreased lipid deposits and lower BW found in the EM strain at the end of lay. 4) Similarly, the suggested lower feed intake may have increased the likelihood of a limiting nutrient on egg production. Calcium

deficiency has been shown to reduce feed intake (Ruschkowski and Hart, 1992), and decrease egg production (Gilbert *et al.*, 1981), although the mechanism by which this occurs has not been fully explored. Taylor (1965) suggested that egg production ceases with calcium deficiency as a result of decreased diffusible calcium levels in the blood. Hypothalamic stimulation of the anterior pituitary is reduced and causes a reduction in gonadotrophin secretion. Luck and Scanes (1979) proposed that either calcium deficiency caused hypothalamic insensitivity to progesterone or resulted in an insufficient storage of LHRH in the hypothalamic neurosecretory cells. In either case, the ionic concentration of plasma calcium may fall below a certain threshold during egg shell calcification and reduce the secretion of gonadotrophins, effectively slowing the rate of follicular growth. As follicular growth slows, there would be a reduction in the rates of estrogen secretion and yolk synthesis by the liver, and the net result would be a reduction in egg production. (Taylor, 1972). Gilbert *et al.* (1981) suggested that any level of dietary calcium less than 35 g/kg would have an adverse effect on egg production, however slight it may be. These authors also observed a higher incidence of cage layer fatigue with diets containing middle values of calcium content (2, 5, 10 g Ca/kg) compared to diets containing higher (≥ 20 g Ca/kg) and lower values (≤ 1 g Ca/kg). As previously mentioned, the EM strain in this experiment demonstrated symptoms of cage layer fatigue at 35 wk of age, which were alleviated upon supplementation of oyster shell in the diet. The layer diet was formulated to provide 3.8 % or 38 g Ca/kg (Table II-1) meeting or exceeding dietary levels specified by the strain management guides when assuming 100-104 g/bird/d feed intake (Anonymous, 1991; 1993).

A reduction in the rate of yolk synthesis and therefore follicular maturation is one possible mechanism by which calcium deficiency may have contributed to shorter prime sequence lengths in the EM strain. Another theoretical possibility is that a mechanism exists by which oviposition is delayed. The calcification process is associated with a decline in plasma concentrations of both total and ionized calcium (Hertelendy and Taylor, 1961; Taylor and Hertelendy, 1961). If either the production or reception of prostaglandins required to

stimulate oviposition were dependent on some threshold ionic calcium level or accumulation, reduced plasma calcium could delay oviposition, increase time in the shell gland, and allow more calcium to be deposited as shell. Since ovulation generally occurs only after the previous oviposition by about 30 min (Melek *et al.* 1973), increased time in the oviduct would effectively improve shell quality, increase lag time between ovipositions and shorten egg-laying sequence lengths as the "open period" for LH is exceeded. This hypothetical mechanism would explain the decreased egg production without alterations in shell quality observed in calcium deficient hens (Gilbert *et al.*, 1981). It could also explain the observation of increased numbers of abnormally-shaped eggs if the hen failed to delay ovulation until after oviposition and more than one egg was forming in the oviduct at a given time.

A small depression in sequence length at peak egg production was observed in the EM strain (Figure II-3). The EM strain hens also demonstrated more shell defects, a higher incidence of defective eggs, and symptoms of cage layer fatigue at 35 wk of age. It would therefore seem likely, that the reduction in average and prime sequence length, as well as sequence profile, may have been a result of the EM strain reaching some limitation of its body energy reserves or a dietary nutrient such as calcium.

The results observed in this experiment indicate that high total egg production was primarily a function of higher rates of lay throughout the laying period to 68 wk, rather than earlier sexual maturity. On a flock basis, normal egg production was not correlated with age at first oviposition ($p = 0.690$, unpublished data) but showed a strong positive correlation with prime sequence length ($r = 0.537$). Prime sequence length displayed a low negative correlation with 18 wk BW ($r = -0.218$). Earlier sexual maturity would not appear to be an effective method to increase marketable egg production, but rather selection under industry conditions using a trait (such as prime sequence length) which effectively isolates the hens with the ability to maintain production of one quality egg per day for extended lengths of time. The probability that dietary nutrient content effectively limited sequence lengths in the lower body weight EM strain serves to emphasize the importance of strain-specific

management in order to achieve these hens' full genetic production potential.

II.4 TABLES AND FIGURES

Table II-1. Diet schedule and nutrient analysis

Nutrients	Starter 0-6 wk	Grower 1 6-12 wk	Grower 2 12-16 wk	Pre-lay 16-20 wk	Layer >20 wk
Crude Protein (%)	21	17	15	16	19
ME (kcal/kg)	2900	2800	2750	2800	2875
Linoleic Acid (%)	1.20	1.00	0.80	1.29	1.40
Methionine (%)	0.42	0.36	0.34	0.39	0.40
Lysine (%)	1.00	0.75	0.70	0.75	0.84
Calcium (%)	0.90	0.95	0.95	2.50	3.80

Table II-2. Carcass and reproductive morphometrics in two strains of Single Comb White Leghorn pullets at sexual maturity (B-group)

Trait	EM[1]	LM[2]	SEM[3]
Age at 1st oviposition (d)	137.5[b]	142.1[a]	1.2
Duration from photostimulation to 1st oviposition (d)	11.5[b]	16.1[a]	1.2
Body weight - fasted (g)	1405[b]	1456[a]	16
Shank length (mm)	98.0	97.4	0.4
Breast muscle weight (g)	188.6[b]	204.1[a]	3.3
Fat pad weight (g)	38.0	39.8	2.1
Liver weight (g)	28.3	28.0	1.5
Oviduct weight (g)	46.9[a]	42.4[b]	1.2
Ovary weight (g)	36.2	33.3	2.2
Stroma weight (g)	3.91	3.89	0.26
Breast muscle weight relative to BW (%)	13.4[b]	14.0[a]	0.2
Fat pad weight relative to BW (%)	2.70	2.71	0.13
Liver weight relative to BW (%)	2.01	1.91	0.10
Oviduct weight relative to BW (%)	3.34[a]	2.91[b]	0.08
Ovary weight relative to BW (%)	2.57	2.29	0.15
Stroma weight relative to BW (%)	0.28	0.27	0.02
Quantity of small yellow follicles (SYF)	5.0	5.2	0.8
Quantity of large yellow follicles (LYF)	7.0	6.4	0.5
Quantity of post-ovulatory follicles (POF)	2.4	2.5	0.1
Total LYF weight (g)	32.3	29.4	0.3
Dried liver weight (g)	17.8	18.0	1.0
Liver lipid content (% DM)	30.8	32.4 (n=18)	4.1
Liver lipid weight (g)	6.11	6.66 (n=18)	1.24
Plasma lipid content (%)	4.16 (n=18)	3.51 (n=19)	0.30
Plasma estradiol-17β content (pg/ml)	114.5 (n=18)	109.1	9.9

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for lowest n. n = 20 unless otherwise specified.

[a,b] Means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-3. Carcass weight and shank length development in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	BW (g)			Shank length (mm)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	1120	1117	16	98.8	98.0	0.8
18	1192	1192	16	97.9	99.5	0.8
19	1334[a]	1262[b]	17	99.1	97.1	0.9
20	1365	1379	23	97.4	97.4	0.6
21	1436	1440	40	98.1	97.2	0.9
22	1399[b]	1493[a]	27	96.6	96.8	0.8
23	1490	1469	25	98.7	97.4	0.8

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-4. Breast muscle development in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	Breast muscle weight (g)			Breast muscle relative to BW (%)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	155.6	163.5	3.6	13.9[b]	14.6[a]	0.2
18	164.4	183.8	7.1	13.8	15.4	0.6
19	192.0[a]	186.2[b]	1.9	14.4	14.8	0.2
20	191.0	201.4	4.5	14.0	14.6	0.3
21	185.8	201.5	6.4	12.9[b]	14.0[a]	0.2
22	170.4[b]	193.7[a]	5.0	12.2	13.0	0.3
23	179.1	189.3	4.8	12.0	12.9	0.3

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-5. Oviduct development in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	Oviduct weight (g)			Oviduct weight relative to BW (%)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	7.4	5.1	1.0	0.66	0.45	0.09
18	14.5	7.1	2.6	1.18[a]	0.60[b]	0.20
19	34.1[a]	14.4[b]	3.0	2.54[a]	1.13[b]	0.21
20	38.2	32.6	3.6	2.81	2.34	0.26
21	56.8[a]	40.7[b]	2.6	4.01[a]	2.82[b]	0.21
22	57.5[a]	50.7[b]	1.8	4.11[a]	3.40[b]	0.10
23	54.3	55.5	3.1	3.87	3.78	0.13

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-6. Carcass and reproductive morphometrics in two strains of Single Comb White Leghorn hens at 68 wk of age (C-group)

Trait	EM[1]	LM[2]	SEM[3]
BW (g)	1690[b]	1994[a]	27
Shank length (mm)	99.06	99.61	0.32
Breast muscle weight (g)	189.1[b]	235.1[a]	4.5
Fat pad weight (g)	79.0[b]	118.2[a]	4.6
Liver weight (g)	32.0[b]	40.7[a]	1.4
Oviduct weight (g)	68.7	66.5	1.2
Ovary weight (g)	51.7	54.5	1.2
Stroma weight (g)	8.68	8.26	0.85
Breast muscle weight relative to BW (%)	11.17[b]	11.81[a]	0.17
Fat pad weight relative to BW (%)	4.58[b]	5.84[a]	0.19
Liver weight relative to BW (%)	1.89	2.02	0.06
Oviduct weight relative to BW (%)	4.10[a]	3.36[b]	0.08
Ovary weight relative to BW (%)	3.08[a]	2.75[b]	0.07
Stroma weight relative to BW (%)	0.51	0.42	0.04
Quantity of small yellow follicles (SYF)	11.5[b]	14.5[a]	0.7
Quantity of large yellow follicles (LYF)	5.2	5.3	0.1

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for lowest n. EM: n=50; LM: n=51.

[a,b] Means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-7. Abdominal fat pad growth in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	Fat pad weight (g)			Fat pad weight relative to BW (%)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	10.8	6.7	1.9	0.95	0.59	0.17
18	22.4[a]	10.1[b]	1.9	1.86[a]	0.84[b]	0.14
19	29.3[a]	22.8[b]	2.1	2.19	1.80	0.15
20	39.2	34.1	2.7	2.86	2.45	0.17
21	41.4	42.6	4.0	2.83	2.95	0.21
22	42.0	47.7	4.3	2.99	3.16	0.26
23	56.5[a]	45.7[b]	3.0	3.78[a]	3.11[b]	0.17

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-8. Liver development in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	Liver weight (g)			Liver weight relative to BW (%)			Dried liver weight (g)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM	EM	LM	SEM
17	19.6	19.1	0.8	1.75	1.71	0.06	13.1	12.9	0.3
18	22.5	20.6	1.0	1.88	1.72	0.07	14.2[a]	13.2[b]	0.3
19	29.8	25.0	2.1	2.23	1.96	0.14	19.4	16.4	1.5
20	31.7	29.5	2.0	2.32	2.12	0.12	19.2	18.7	1.6
21	31.6	28.2	3.9	2.14	1.95	0.20	20.0	18.0	2.8
22	24.8	25.2	1.3	1.76	1.68	0.07	15.7	15.6	0.8
23	27.6[a]	22.8[b]	0.7	1.85[a]	1.55[b]	0.04	15.9[a]	14.1[b]	0.4

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-9. Ovary development in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

Age (wk)	Ovary weight (g)			Ovary weight relative to BW (%)		
	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	0.9[a]	0.7[b]	0.1	0.08[a]	0.06[b]	0.01
18	3.2	0.6	1.1	0.25	0.05	0.08
19	16.9[a]	1.7[b]	3.2	1.24[a]	0.13[b]	0.23
20	26.5	14.5	5.8	1.96	1.03	0.42
21	45.5[a]	24.5[b]	4.6	3.23[a]	1.68[b]	0.34
22	49.3[a]	36.9[b]	2.3	3.53[a]	2.47[b]	0.15
23	55.4	49.4	2.9	3.72	3.36	0.19

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-10. Stroma development in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	Stroma weight (g)			Stroma weight relative to BW (%)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	0.85[a]	0.65[b]	0.06	0.076[a]	0.058[b]	0.005
18	0.96[a]	0.62[b]	0.11	0.079[a]	0.052[b]	0.008
19	2.58[a]	1.14[b]	0.19	0.193[a]	0.089[b]	0.014
20	3.56[a]	2.01[b]	0.47	0.262[a]	0.145[b]	0.035
21	5.25[a]	2.23[b]	0.39	0.377[a]	0.155[b]	0.034
22	5.59[a]	3.46[b]	0.34	0.399[a]	0.233[b]	0.023
23	7.10[a]	5.69[b]	0.37	0.479[a]	0.389[b]	0.028

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851
[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9
[3] SEM listed for n = 10.
[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-11. Quantity of small yellow follicles (SYF) and quantity and total weight of large yellow follicles (LYF) in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	SYF			LYF			Total LYF weight (g)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM	EM	LM	SEM
17	0.3	0.0	0.2	0.1	0.0	0.1	0.1	0.0	0.1
18	0.3	0.0	0.2	0.9	0.0	0.4	2.1	0.0	1.0
19	4.1[a]	0.5[b]	0.6	4.0[a]	0.3[b]	0.8	14.4[a]	0.6[b]	3.1
20	3.7	2.0	0.7	5.7	3.0	1.3	23.0	12.5	5.4
21	9.6[a]	3.0[b]	1.0	8.5[a]	4.2[b]	0.6	40.3[a]	23.3[b]	4.3
22	7.8[a]	3.5[b]	0.8	8.0[a]	6.5[b]	0.4	43.8[a]	33.4[b]	2.4
23	12.1[a]	8.6[b]	1.0	8.5[a]	6.9[b]	0.3	48.3	43.7	2.9

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851
[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9
[3] SEM listed for n = 10.
[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-12. Plasma estradiol-17β and plasma lipid concentration in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

	Plasma Estradiol-17β (pg/ml)			Plasma Lipid (%)		
Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	91.8	75.9	12.1	0.68	0.61	0.07
18	119.3	95.4	17.5	1.35[a]	0.60[b]	0.24
19	163.0	154.6	16.9	3.86[a]	1.05[b]	0.53
20	141.6	169.0	25.9	4.51[a]	2.50[b]	0.59
21[4]	--	--	--	4.90	4.21	0.76
22	--	--	--	2.79	3.69	0.48
23	--	--	--	3.29	2.95	0.40

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for n = 10.

[4] Estradiol-17β RIA was only performed on Group A-17, A-18, A-19 and A-20 plasma samples.

[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-13. Liver lipid content in two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

Age (wk)	Liver lipid content (% DM)			Liver lipid weight (g)		
	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
17	12.74[a]	10.95[b]	0.52	1.67[a]	1.41[b]	0.09
18	15.22[a]	10.02[b]	1.42	2.23[a]	1.32[b]	0.26
19	36.64	21.88	5.82	7.93	4.32	1.74
20	33.85	33.61	5.79	7.25	7.04	1.76
21	28.26	33.61	6.62	7.97	6.84	2.83
22	17.56	24.68	3.55	2.67	4.30	0.90
23	22.40	16.62	2.16	3.67	2.34	0.45

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851
[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9
[3] SEM listed for n = 10.
[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-14. Carcass composition (weight basis) for two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
	Moisture weight (g)			Protein weight (g)		
17	695.8	693.3	14.5	256.1	271.2	7.6
18	728.6	744.6	10.6	270.5	287.1	7.7
19[4]	753.4	730.6	10.9	315.1	303.1	4.6
20	738.0	762.9	9.6	313.7	317.6	4.1
21	784.7	778.2	15.6	309.6	319.1	7.9
22	747.8	792.8	18.9	312.6	320.8	9.1
23	773.2	766.8	12.6	310.9	323.5	5.2
	Lipid weight (g)			Ash weight (g)		
17	85.4	67.8	8.5	40.2	40.9	1.4
18	112.5[a]	83.3[b]	7.1	40.7	41.0	1.6
19	170.2[a]	139.4[b]	7.1	48.9[a]	44.8[b]	1.2
20	211.6	198.1	11.5	48.8	47.4	1.5
21	226.3	230.0	15.0	42.2	43.6	2.0
22	227.7	246.3	17.0	43.5	47.9	2.3
23	284.6[a]	248.9[b]	9.8	44.3	45.6	2.0

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851
[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9
[3] SEM listed for n = 10, unless otherwise specified.
[4] SEM listed for n = 9, for carcass composition of Group A-19, EM strain.
[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-15. Carcass composition (percentage basis) of two strains of Single Comb White Leghorn pullets at 17 to 23 wk of age (A-Group)

Age (wk)	EM[1]	LM[2]	SEM[3]	EM	LM	SEM
	Moisture content (%)			Protein content (%)		
17	64.19	64.30	1.14	23.60	25.19	0.69
18	62.86	64.15	0.98	23.27	24.73	0.55
19[4]	58.17	59.67	0.58	24.32	24.78	0.31
20	55.93	57.07	0.46	23.78	23.75	0.23
21	57.38	56.43	0.61	22.58	23.15	0.32
22	55.84	56.08	1.24	23.34	22.64	0.50
23	54.35	54.98	0.40	21.87[b]	23.21[a]	0.33
	Lipid content (%)			Ash content (%)		
17	7.83	6.27	0.76	3.71	3.81	0.13
18	9.63[a]	7.16[b]	0.54	3.48	3.55	0.12
19	13.11[a]	11.38[b]	0.51	3.77	3.66	0.08
20	15.97	14.73	0.68	3.72	3.55	0.11
21	16.26	16.63	0.66	3.06	3.16	0.11
22	16.95	17.23	1.01	3.26	3.37	0.13
23	19.93[a]	17.85[b]	0.50	3.12	3.26	0.13

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851
[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9
[3] SEM listed for n = 10, unless otherwise specified.
[4] SEM listed for n = 9, for carcass composition of Group A-19, EM strain.
[a,b] For each trait, means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-16. Carcass composition in two strains of Single Comb White Leghorn pullets at sexual maturity (B-group)

Trait	EM[1]	LM[2]	SEM[3]
Moisture (%)	57.26	58.04	0.57
Protein (%)	23.24	22.74	0.18
Lipid (%)	15.06	15.22	0.51
Ash (%)	3.66[a]	3.40[b]	0.06
Moisture weight (g)	772.2[b]	816.0[a]	8.6
Protein weight (g)	313.5	320.2	4.1
Lipid weight (g)	203.5	215.2	8.3
Ash weight (g)	49.4	47.8	1.0

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851
[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9
[3] SEM listed for n = 20.
[a,b] Means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-17. Egg production traits of two strains of Single Comb White Leghorn hens at 68 wk of age (C-group)

Trait	EM[1]	LM[2]	SEM[3]
Total eggs produced	296.5	298.8	2.5
Duration from 1st egg to 68 wk (d)	336.2[a]	330.4[b]	0.8
Average hen-day production 1[4] (%)	84.7	85.4	0.7
Average hen-day production 2[5] (%)	88.2[b]	90.4[a]	0.7
Prime sequence length (d)	52.6[b]	71.4[a]	5.2
Normal shelled eggs	284.8[b]	294.6[a]	3.2
Soft shelled eggs	3.78[a]	1.23[b]	0.90
Shell-less eggs	2.28[a]	0.96[b]	0.41
Double-yolked eggs	3.06[a]	0.81[b]	0.28
Abnormal shelled eggs	2.60	1.21	0.67
Broken eggs	0.08	0.12	0.05
Pecked eggs	0.02	0.04	0.02
First egg weight (g)	40.7	39.4	0.1
Last egg weight (g)	62.4	63.4	0.7
Number of sequences (d)	39.9[a]	31.2[b]	2.1
Number of pauses (sequences less 1)	38.9[a]	30.2[b]	2.1
Average sequence length (d)	8.7[b]	12.8[a]	1.0
Average pause length (d)	1.16	1.16	0.03

[1] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

[2] LM=Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] SEM listed for lowest n. EM: n=50; LM: n=51.

[4] Hen-day production 1 calculated by egg number / hen-days from photostimulation to 68 wk.

[5] Hen-day production 2 calculated by egg number / hen-days from first oviposition to 68 wk.

[a,b] Means within a row with no common superscript differ significantly ($P < 0.05$).

Table II-18. BW correlation coefficients & p-values[1] on total flock of Single Comb White Leghorn hens (n=100)

	12 wk BW	17 wk BW	18 wk BW	19 wk BW	26 wk BW	34 wk BW	42 wk BW	50 wk BW	58 wk BW	66 wk BW
6 wk BW	0.681 (0.000)	0.265 (0.008)	0.244 (0.014)	0.245 (0.014)	0.384 (0.000)	0.371 (0.000)	0.408 (0.000)	0.404 (0.000)	0.414 (0.000)	0.376 (0.000)
12 wk BW		0.475 (0.000)	0.463 (0.000)	0.478 (0.000)	0.477 (0.000)	0.436 (0.000)	0.435 (0.000)	0.411 (0.000)	0.414 (0.000)	0.378 (0.000)
17 wk BW			0.862 (0.000)	0.694 (0.000)	0.345 (0.000)	0.238 (0.017)	0.289 (0.004)	0.220 (0.028)	0.226 (0.024)	0.124
18 wk BW				0.882 (0.000)	0.356 (0.000)	0.239 (0.017)	0.249 (0.013)	0.205 (0.041)	0.214 (0.032)	0.105
19 wk BW					0.438 (0.000)	0.310 (0.002)	0.315 (0.001)	0.273 (0.006)	0.293 (0.003)	0.186 (0.064)
26 wk BW						0.895 (0.000)	0.834 (0.000)	0.798 (0.000)	0.795 (0.000)	0.670 (0.000)
34 wk BW							0.917 (0.000)	0.870 (0.000)	0.857 (0.000)	0.784 (0.000)
42 wk BW								0.941 (0.000)	0.933 (0.000)	0.849 (0.000)
50 wk BW									0.950 (0.000)	0.871 (0.000)
58 wk BW										0.908 (0.000)

[1] P-values only listed if $p \leq 0.1$

Table II-19 Egg production correlation coefficients & p-values[1] on total flock of Single Comb White Leghorn hens (n=100)

	Age at 1st oviposition	1st egg weight	Total eggs	Normal eggs	Soft shelled eggs	Shell-less eggs	Double-yolked eggs	Abnormal shelled eggs	Prime seq[2] length	Number of seq's	Average seq length	Average pause length
18 wk BW	-0.503 (0.000)	-0.074	-0.004	-0.107	0.115	0.025	0.217 (0.030)	0.230 (0.022)	-0.218 (0.029)	0.217 (0.030)	-0.150	0.078
Age at 1st oviposition		0.269 (0.007)	-0.238 (0.017)	-0.040	-0.162	-0.070	-0.420 (0.000)	-0.244 (0.014)	0.080	-0.145	0.093	-0.071
1st egg weight			-0.153	-0.079	-0.041	0.016	-0.066	-0.117	0.023	0.016	0.004	0.003
Total eggs				0.851 (0.000)	-0.199 (0.047)	-0.084	0.062	-0.050	0.530 (0.000)	-0.772 (0.000)	0.703 (0.000)	-0.346 (0.000)
Normal eggs					-0.624 (0.000)	-0.405 (0.000)	-0.197 (0.050)	-0.442 (0.000)	0.537 (0.000)	-0.859 (0.000)	0.682 (0.000)	-0.353 (0.000)
Soft-shelled eggs						0.479 (0.000)	0.187 (0.063)	0.536 (0.000)	-0.211 (0.035)	0.453 (0.000)	-0.212 (0.035)	0.138
Shell-less eggs							0.389 (0.000)	0.201 (0.045)	-0.110	0.311 (0.002)	-0.177 (0.078)	0.065
Double-yolked eggs								0.221 (0.027)	-0.127	0.147	-0.165 (0.102)	0.117
Abnormal shelled eggs									-0.184 (0.067)	0.369 (0.000)	-0.171 (0.089)	0.119
Prime seq length										-0.680 (0.000)	0.688 (0.000)	-0.012
Number of seq's											-0.814 (0.000)	0.064
Average seq length												-0.120

[1] P-values only listed if $p \leq 0.1$
[2] Seq = Egg laying sequence

Table II-20. Egg production correlation coefficients & p-values[1] for LM[2] strain of Single Comb White Leghorn hens (n=51)

	Age at 1st oviposition	1st egg weight	Total eggs	Normal eggs	Soft shelled eggs	Shell-less eggs	Double-yolked eggs	Abnormal shelled eggs	Prime seq[3] length.	Number of seq's	Average seq length	Average pause length
18 wk BW	-0.431 (0.002)	-0.194	-0.118	-0.177	0.282 (0.045)	0.249 (0.078)	0.114	0.067	-0.272 (0.053)	0.264 (0.061)	-0.223	0.113
Age at 1st oviposition		0.343 (0.014)	-0.206	-0.165	-0.139	0.102	-0.183	-0.079	0.070	-0.085	0.040	-0.100
1st egg weight			-0.044	0.023	-0.283 (0.044)	-0.135	0.085	-0.181	0.060	-0.066	0.096	-0.250 (0.077)
Total eggs				0.957 (0.000)	-0.068	-0.078	-0.092	0.044	0.578 (0.000)	-0.856 (0.000)	0.725 (0.000)	-0.347 (0.013)
Normal eggs					-0.256 (0.070)	-0.221	-0.271 (0.054)	-0.195	0.603 (0.000)	-0.833 (0.000)	0.728 (0.000)	-0.384 (0.005)
Soft-shelled eggs						0.534 (0.000)	0.251 (0.076)	0.228	-0.153	0.125	-0.136	0.172
Shell-less eggs							0.159	0.028	0.037	0.082	-0.072	0.061
Double-yolked eggs								0.451 (0.001)	-0.177	0.158	-0.182	0.125
Abnormal shelled eggs									-0.187	-0.026	-0.065	0.147
Prime seq length										-0.721 (0.000)	0.715 (0.000)	-0.083
Number of seq's											-0.843 (0.000)	0.070
Average seq length												-0.060

[1] P-values only listed if $p \leq 0.1$

[2] LM–Later Maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[3] Seq – Egg laying sequence

Table II-21. Egg production correlation coefficients & p-values[1] for EM[2] strain of Single Comb White Leghorn hens (n=49)

	Age at 1st oviposition	1st egg weight	Total eggs	Normal eggs	Soft shelled eggs	Shell-less eggs	Double-yolked eggs	Abnormal shelled eggs	Prime seq[3] length.	Number of seq's	Average seq length	Average pause length
18 wk BW	-0.603 (0.000)	-0.034	0.125	-0.029	0.087	-0.098	0.258 (0.074)	0.319 (0.026)	-0.130	0.149	-0.003	0.034
Age at 1st oviposition		0.396 (0.005)	-0.414 (0.003)	-0.166	-0.082	0.028	-0.282 (0.050)	-0.277 (0.054)	-0.189	0.049	-0.211	-0.042
1st egg weight			-0.227	-0.092	-0.047	0.019	-0.217	-0.121	0.063	0.006	-0.002	0.201
Total eggs				0.789 (0.000)	-0.280 (0.051)	-0.074	0.253 (0.080)	-0.110	0.460 (0.001)	-0.711 (0.000)	0.756 (0.000)	-0.349 (0.014)
Normal eggs					-0.761 (0.000)	-0.448 (0.001)	-0.029	-0.557 (0.000)	0.445 (0.001)	-0.875 (0.000)	0.699 (0.000)	-0.357 (0.012)
Soft-shelled eggs						0.460 (0.001)	0.089	0.614 (0.000)	-0.265 (0.066)	0.585 (0.000)	-0.304 (0.034)	0.195
Shell-less eggs							0.362 (0.011)	0.223	-0.133	0.371 (0.009)	-0.209	0.081
Double-yolked eggs								0.070	0.138	-0.081	0.136	0.155
Abnormal shelled eggs									-0.145	0.612 (0.000)	-0.268 (0.062)	0.107
Prime seq length										-0.587 (0.000)	0.537 (0.000)	0.149
Number of seq's											-0.815 (0.000)	0.054
Average seq length												-0.019

[1] P-values only listed if $p \leq 0.1$ [2] EM=Early Maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. PO. Box 280, Ithaca, NY. 14851
[3] Seq = Egg laying sequence

Table II-22 Correlation coefficients & p-values[1] of sequence lengths and carcass traits at 68 wk on total flock of Single Comb White Leghorn hens (n=100).

	Breast muscle weight	Fat pad weight	Liver weight	Oviduct weight	Ovary weight	Number of SYF[2]	Number of LYF[3]	Total eggs	Prime sequence length	Average sequence length	Egg weight at 68 wk
66 wk BW	0.902 (0.000)	0.857 (0.000)	0.706 (0.000)	0.086	0.333 (0.001)	0.091	0.116	-0.070	0.050	0.057	0.252 (0.012)
Breast muscle weight		0.658 (0.000)	0.539 (0.000)	0.044	0.279 (0.005)	0.045	0.039	-0.048	0.105	0.119	0.097
Fat pad weight			0.659 (0.000)	0.017	0.189 (0.060)	0.117	0.079	-0.082	-0.016	-0.049	0.188 (0.061)
Liver weight				-0.062	0.370 (0.000)	0.142	0.186 (0.064)	-0.182 (0.070)	-0.031	-0.038	0.178 (0.077)
Oviduct weight					-0.038	-0.121	0.182 (0.071)	0.067	0.109	-0.023	0.307 (0.002)
Ovary weight						0.070	0.319 (0.001)	0.034	0.218 (0.029)	0.186 (0.065)	0.329 (0.001)
Number of SYF							0.085	0.022	0.025	0.051	0.013
Number of LYF								0.163	0.209 (0.037)	0.146	0.076
Total eggs									0.530 (0.000)	0.703 (0.000)	-0.394 (0.000)
Prime sequence length										0.688 (0.000)	-0.096
Average sequence length											-0.284 (0.004)

[1] P-values only listed if $p \leq 0.1$
[2] SYF = Small yellow follicles
[3] LYF = Large yellow follicles

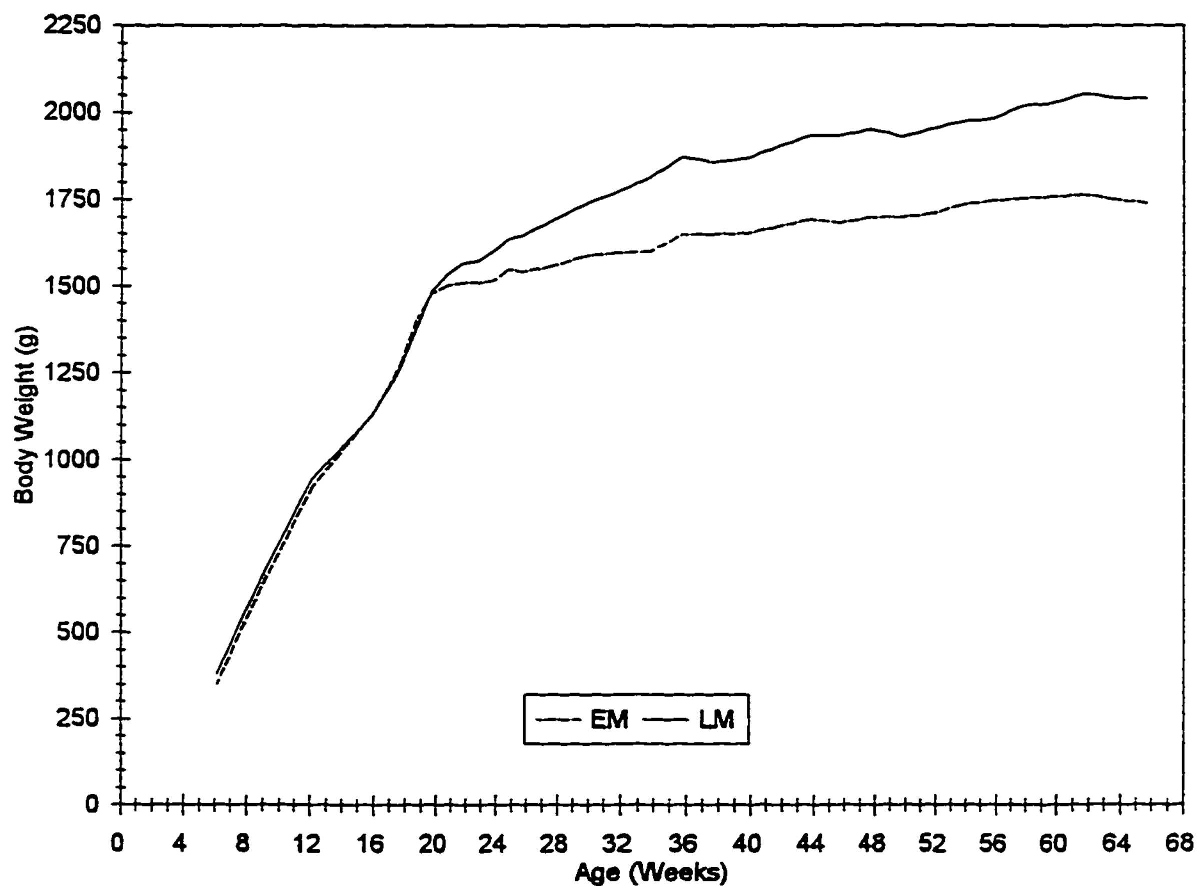

Figure II-1. Increase in BW from rearing to 68 wk in two strains of Single Comb White Leghorn hens differing in age at sexual maturity. BW differed significantly after 24 wk of age ($p < 0.05$). (n=50)

EM = Early maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

LM = Later maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

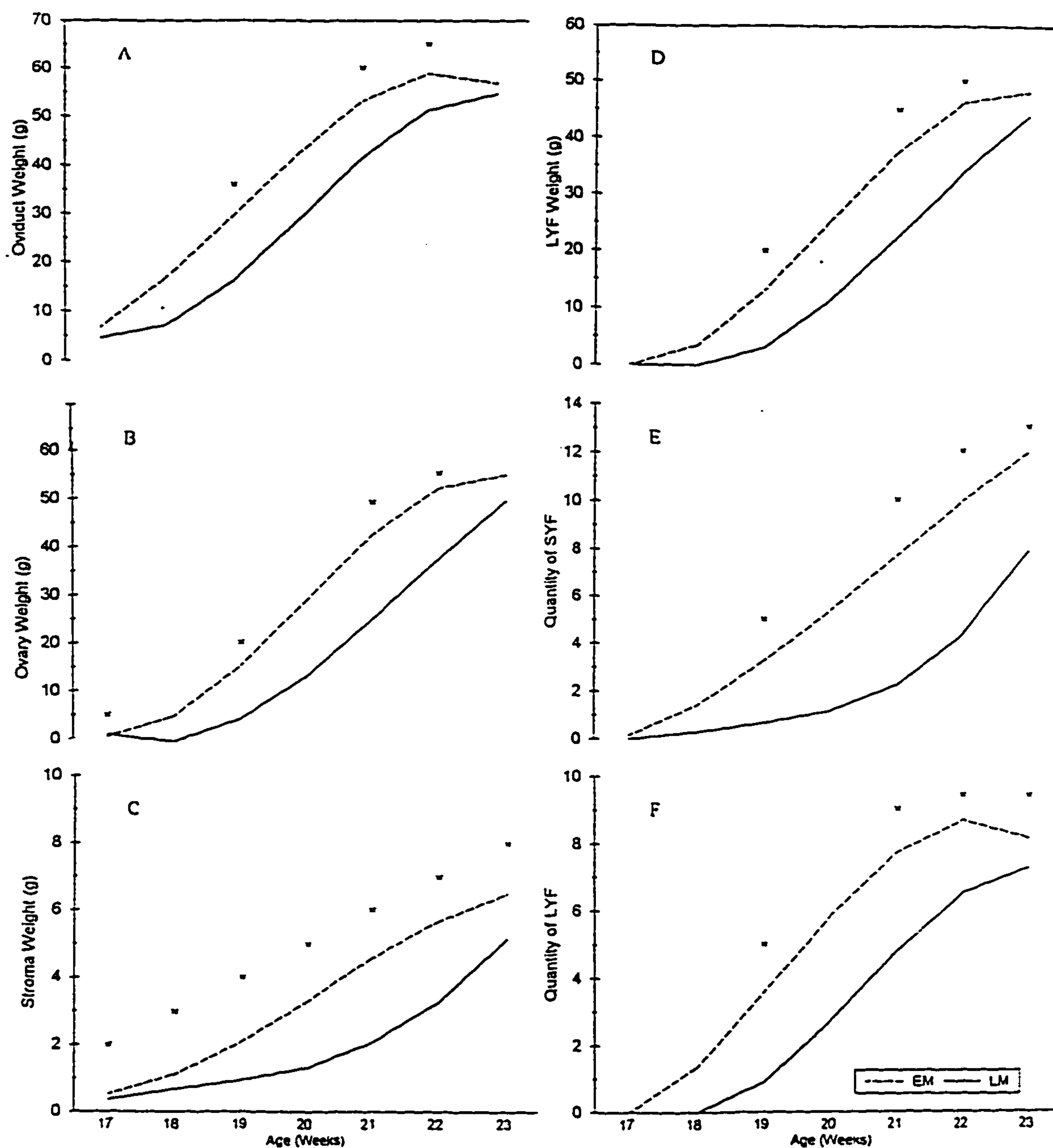

Figure II-2. Reproductive morphometrics from 17 to 23 wk of age[1] in two strains (n=10*7) of Single Comb White Leghorn hens differing in age at sexual maturity. (Panel A: Oviduct wt; B: Ovary wt; C: Stroma wt; D: LYF[2] wt; E: Quantity of SYF[3]; and F: Quantity of LYF). Significant differences between strains for each trait marked by X ($p<0.05$).

EM = Early maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

LM = Later maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, N1R 5V9

[1] Data smoothed with third order regression equations

[2] LYF = Large yellow follicles; [3] SYF = Small yellow follicles

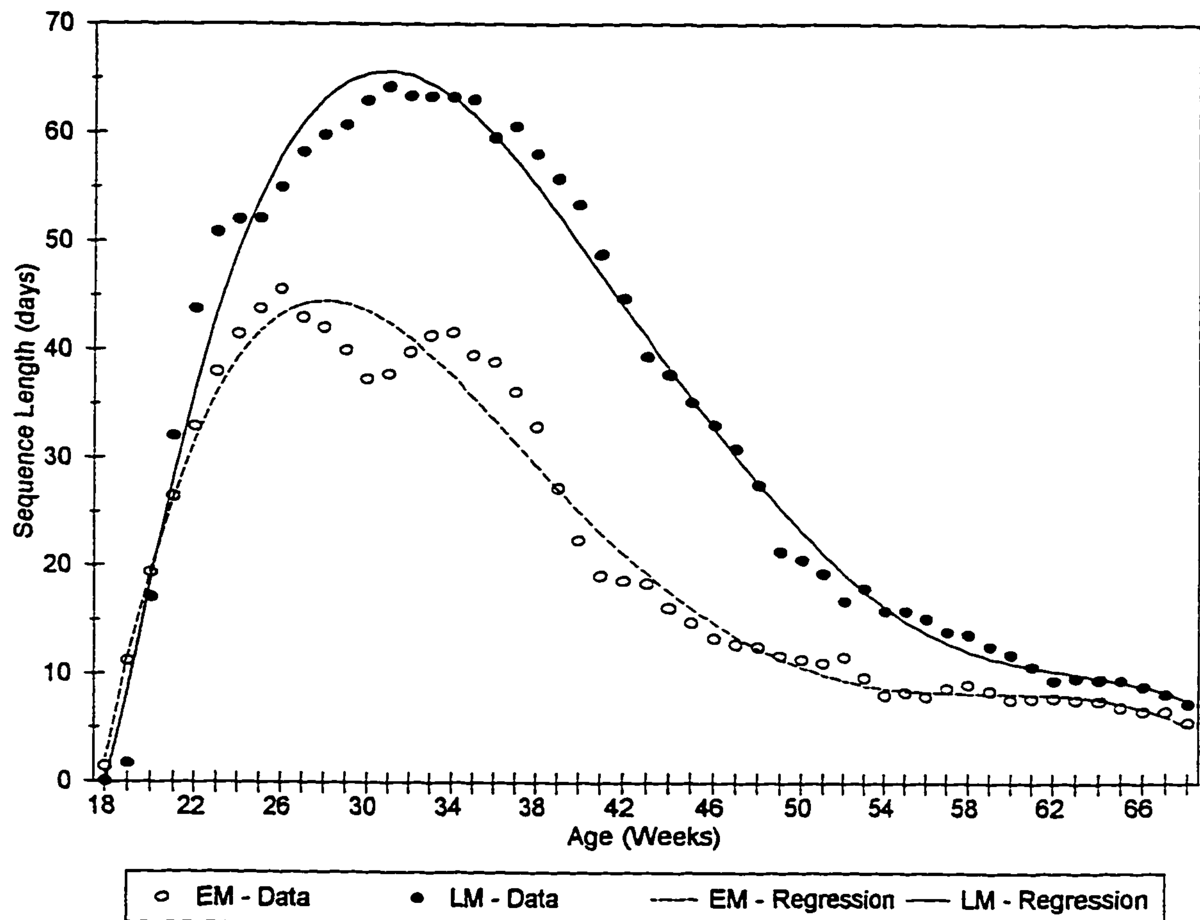

Figure II-3. Sequence length profiles[1] from initiation of lay to 68 wk in two strains of Single Comb White Leghorn hens differing in age at sexual maturity. (n=50)

EM = Early maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

LM = Later maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[1] Data smoothed with fifth order regression equation

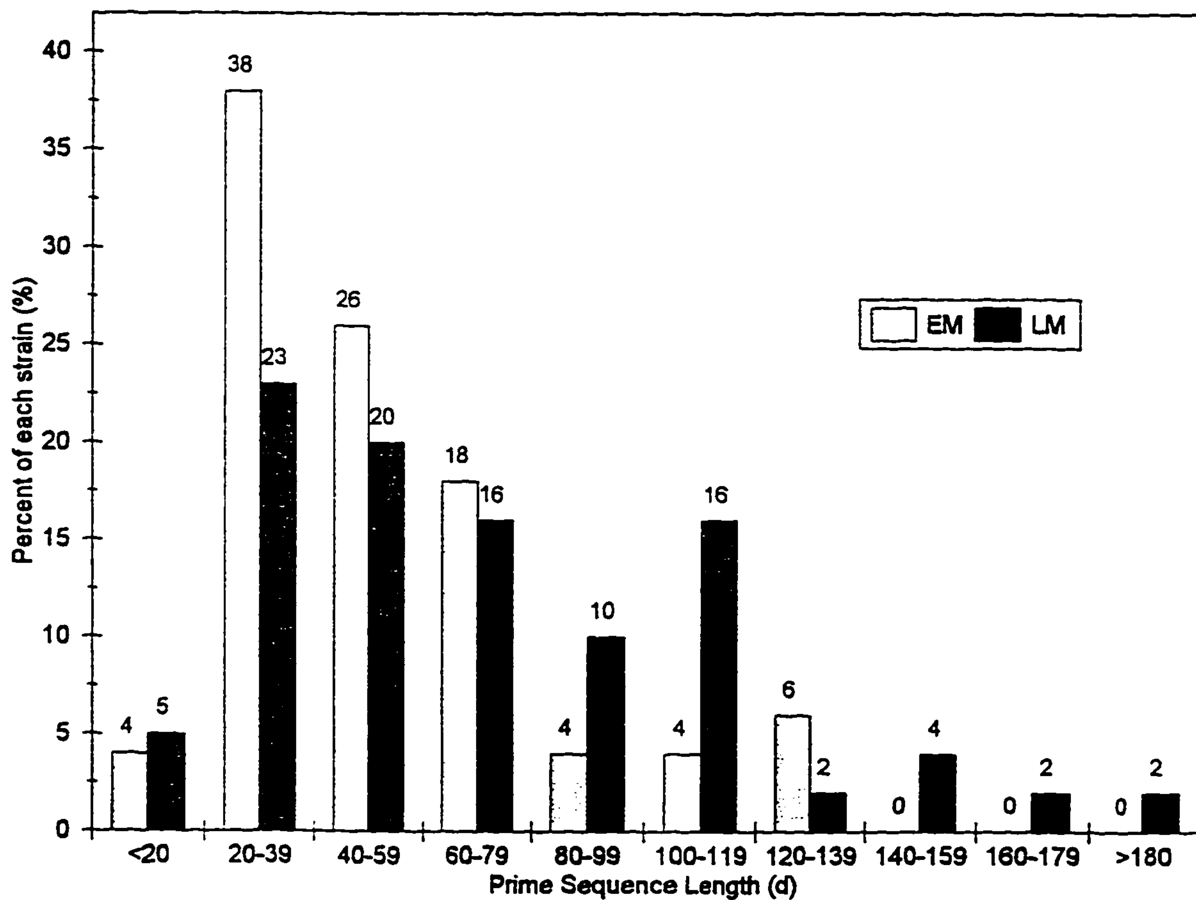

Figure II-4. Percentage of individuals of two strains of Single Comb White Leghorn hens differing in age at sexual maturity grouped by length of prime egg-laying sequence. (n=50)

EM = Early maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

LM = Later maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

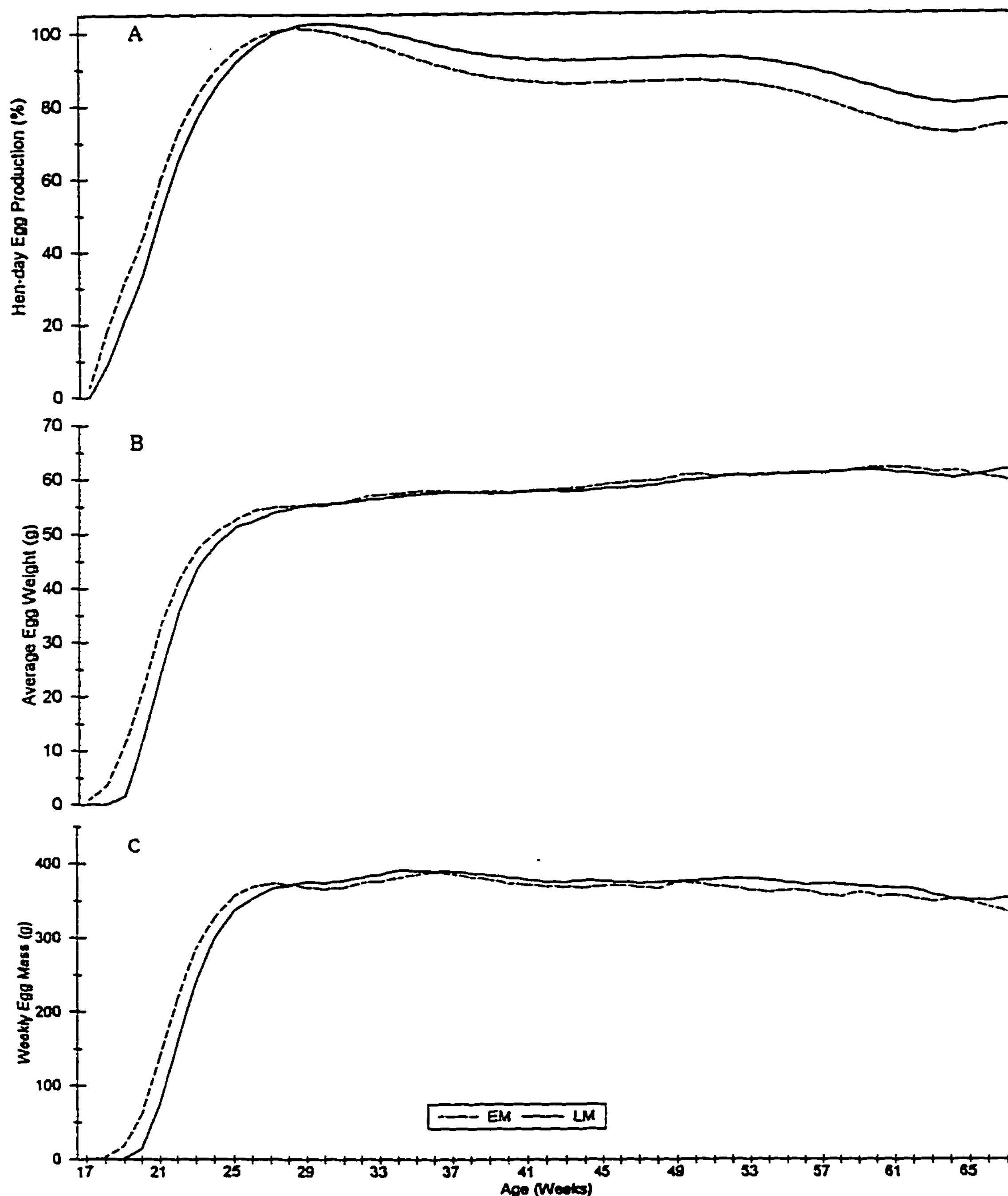

Figure II-5. Weekly hen-day production[1], average egg weight and weekly egg mass production curves from initiation of lay to 68 wk in two strains of Single Comb White Leghorn hens differing in age at sexual maturity. (n=50)

EM = Early maturing, Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

LM = Later maturing, Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada. N1R 5V9

[1] Data smoothed with fifth order regression equation

II.5 REFERENCES CITED

Anonymous, 1991. Shaver White Commercial Management Guide (T-05-I), Shaver Poultry Breeding Farms Limited, Cambridge, Ontario, Canada N1R 5V9.

Anonymous, 1993. ISA Babcock B 300 White Egg Layer Management Guide, North America - 1993 edition. ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY 14851.

Association of Official Analytical Chemists, 1980. Official Methods of Analysis, 13th ed AOAC, Washington, D.C.

Bell, D.D., D.R. Kuney, and C.J. Adams, 1982. Varying the age of sexual stimulation in SCWL pullets. Poultry Sci. 61:1416(Abstr.).

Bhatti, B.M., and T.R. Morris, 1977. The relative importance of light and temperature as phase setting signals for oviposition in the fowl. Br. Poult. Sci. 18: 391-395.

Blake, A.G., and R.K. Ringer, 1987. Changes in Ring-Necked Pheasants' (Phasianus colchicus) egg formation time, oviposition lag time, and egg sequence length due to ahemeral light-dark cycles. Poultry Sci. 66:231-236.

Bohren, B.B., V.A. Garwood, and P.C. Lowe, 1981. Direct and correlated responses to selection for age at maturity in the fowl. Poultry Sci. 60: 289-294.

Bornstein, S., I. Plavnik, and Y. Lev, 1984. Body weight and/or fatness as potential determinants of the onset of egg production in broiler breeder hens. Br. Poult. Sci. 25: 323-341.

Brody, T., Y. Eitan, M. Soller, I. Nir, and Z. Nitsan. 1980. Compensatory growth and sexual maturity in broiler females reared under severe food restriction from day of hatching. Br. Poult. Sci. 21: 437-446.

Brody, T.B., P.B. Siegel, and J.A. Cherry, 1984. Age, body weight, and body composition requirements for the onset of sexual maturity of dwarf and normal chickens. Br. Poult. Sci. 25: 245-252.

Cain, J.R., and W.O. Wilson. 1974. The influence of specific environmental parameters on the circadian rhythms of chickens. Poultry Sci. 53:1438-1447.

Eitan, Y., and M. Soller, 1991. Two-way selection for threshold body weight at first egg in broiler strain females. 2. Effect of supplemental light on weight and age at first egg. Poultry Sci. 70: 2017-2022.

Etches, R.J., 1984. Maturation of ovarian follicles. pp 51-73. *in*: Reproductive Biology of Poultry. Cunningham, F.J., Lake, P.E., and D. Hewitt, eds. British Poultry Science Ltd.

Etches, R.J., 1990. The ovulatory cycle of the hen. CRC Crit. Rev. Poult. Biol. 2: 293-318.

Etches, R.J., 1996. Reproduction in Poultry. CAB International. Wallingford, UK.

Etches, R.J., and J.P. Schoch, 1984. A mathematical representation of the ovulatory cycle of the domestic hen. Br. Poult. Sci. 25: 65-76.

Fairfull, R.W., and R.S. Gowe, 1990. Genetics of egg production in chickens. pp 705-760. *in*: Poultry Breeding and Genetics. R.D. Crawford, ed. Elsevier, Amsterdam.

Fraps, R.M., 1955. Egg production and fertility in poultry. p 661. *in*: Progress in the Physiology of Farm Animals, Vol. 2., J. Hammond, eds. Buttorworths Scientific, London.

Gilbert, A.B., 1971. The ovary. pp 1163-1208. *in*: Physiology and Biochemistry of the Domestic Fowl, Vol. 3. Bell, D.J., and B.M. Freeman, ed. Academic Press, London.

Gilbert, A.B., J. Peddie, G.G. Mitchell, and P.W. Teague, 1981. The egg-laying response of the domestic hen to variation in dietary calcium. Br. Poult. Sci. 22: 537-548.

Gilbert, A.B., M.M. Perry, D. Waddington, and M.A. Hardie, 1983. Role of atresia in establishing the follicular hierarchy in the ovary of the domestic hen (*Gallus domesticus*). J. Reprod. Fertil. 69: 221-227.

Gow, C.B., P.J. Sharp, N.B. Carter, R.J. Scaramuzzi, B.L. Sheldon, B.H. Yoo, and R.T. Talbot., 1985. Effects of selection for reduced oviposition interval on plasma concentrations of luteinizing hormone during the ovulatory cycle in hens on a 24 h lighting cycle. Br. Poult. Sci. 26: 441-451.

Harrison, P.C., G. Schmaier, and J. McGinnis, 1969. Reproductive development and response of White Leghorn pullets subjected to increasing daylengths at different ages. Poultry Sci. 48:1021-1026.

Hertelendy, F., and T.G. Taylor, 1961. Changes in blood calcium associated with egg shell calcification in the domestic fowl. 1. Changes in the total calcium. Pcultry Sci. 40: 108-114.

Hocking, P.M., A.B. Gilbert, M.A. Walker, and D. Waddington, 1987. Ovarian follicular structure of white leghorns fed *ad libitum* and dwarf and normal broiler breeders fed *ad libitum* or restricted to point of lay. Br. Poult. Sci. 28: 493-506.

Hocking, P.M., D. Waddington, M.A. Walker, and A.B. Gilbert, 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. Br. Poult. Sci. 30: 161-173.

Hunton, P., 1990. Industrial breeding and selection. pp 985-1028. *in*: Poultry Breeding and Genetics. R.D. Crawford, ed. Elsevier, Amsterdam.

Keshavarz, K., and S. Nakajima, 1993. Re-evaluation of calcium and phosphorus requirements of laying hens for optimum performance and eggshell quality. Poultry Sci. 72: 144-153.

Kling, L.J., R.O. Hawes, R.W. Gerry, and W.A. Halteman, 1985. Effects of early maturation of brown egg-type pullets, flock uniformity, layer protein level, and cage design on egg production, egg size, and egg quality. Poultry Sci. 64:1050-1059.

Luck, M.R., and C.G. Scanes, 1979. The relationship between reproductive activity and blood calcium in the calcium-deficient hen. Br. Poultry Sci. 20: 559-564.

Lupicki, M.E., 1994. Ovarian morphology and steroidogenesis in domestic fowl (*Gallus domesticus*): Effects of aging, strain, photostimulation program and level feeding. M.Sc. Thesis, University of Alberta.

McClung, M.R., A.B.S. Wang, and W.T. Jones, 1976. Response to selection for time interval between ovipositions in the hen. Poultry Sci. 55: 160-171.

McMillan, I., R.W. Fairfull, R.S. Gowe, and J.S. Gavora, 1990. Evidence for genetic improvement of layer stocks of chickens during 1950-80. Wld's Poultry Sci. J. 46:235-245.

Melek, O., T.R. Morris, and R.C. Jennings, 1973. The time factor in egg formation for hens exposed to ahemeral light-dark cycles. Br. Poult. Sci. 14:493-498.

Morris, T.R., 1994. Lighting for layers: what we know and what we need to know. Wld's Poultry Sci. J. 50:283-287.

Robinson, F.E., 1993. A study of mortality, egg quality, and egg production in Alberta table egg production units. Alberta Agric. Res. Institute. Project # AARI90M227.

Robinson, F.E., R.T. Hardin, and A.R. Robblee, 1990. Reproductive senescence in domestic fowl: Effects on egg production, sequence length and inter-sequence pause length. Br. Poult. Sci. 31:871-879.

Robinson, F.E., N.A. Robinson, and T.A. Scott, 1991. Reproductive performance, growth rate, and body composition of full-fed versus feed-restricted broiler breeder hens. Can. J. Anim. Sci. 71: 549-556.

Robinson, F.E., T.A. Wautier, R.T. Hardin, J.L. Wilson, M. Newcombe, and R.I. McKay, 1996a. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 1. Broiler breeder hens. Can. J. Anim. Sci. 76: 275-282.

Robinson, F.E., T.A. Wautier, R.T. Hardin, J.L. Wilson, M. Newcombe, and R.I. McKay, 1996b. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 2. Egg-type hens. Can. J. Anim. Sci. 76: 283-288.

Robinson, F.E., J.L. Wilson, M.W. Yu, G.M. Fasenko, and R.T. Hardin, 1993. The relationship between body weight and reproductive efficiency in meat-type chickens. Poultry Sci. 72: 912-922.

Ruschkowski, S.R., and L.E. Hart, 1992. Ionic and endocrine characteristics of reproductive failure in calcium-deficient and vitamin D-deficient laying hens. Poultry Sci. 71: 1722-1732.

SAS Institute, 1992. The SAS® System for Windows 3.10. Release 6.08. Cary, N.C.

Siopes, T.D., 1992. Effects of age at lighting on reproduction of turkey hens. Poultry Sci. 71:2099-2105.

Soller, M., T. Brody, Y. Eitan, T. Agursky, and C. Wexler, 1984. Minimum weight for onset of sexual maturity in chickens: Heritability and phenotypic and genetic correlations with early growth rate. Poultry Sci. 63: 2103-2113.

Summers, J.D., and S. Leeson, 1983. Factors influencing early egg size. Poultry Sci. 62:1155-1159.

Taylor, T.G., 1965. Calcium-endocrine relationships in the laying hen. Proc. Nutr. Soc. 24: 49-54.

Taylor, T.G., 1972. The role of calcium in egg production. Pages 107-111 *in:* Egg Formation and Production, Freeman, B.M., and P.E. Lake, eds. Edinburgh, British Poultry Science Ltd.

Taylor. T.G., and F. Hertelendy, 1961. Changes in blood calcium associated with egg shell calcification in the domestic fowl. 1. Changes in the diffusible calcium. Poultry Sci. 40: 115-123.

van Middelkoop, J.H., 1972. The relationship between ovulation interval of White Plymouth Rock pullets and the laying of abnormal eggs. Arch. Geflügelkd. 36: 223-230.

Waddington, D., M.M. Perry, A.B. Gilbert, and M.A. Hardie, 1985. Follicular growth and atresia in the ovaries of hens (*Gallus domesticus*) with diminished egg production rates. J. Reprod. Fertil. 74: 399-405.

Warren, D.C., and H.M. Scott, 1935. The time factor in egg formation. Poultry Sci. 14: 195-207.

Williams, J.B., and P.J. Sharp, 1978. Ovarian morphology and rates of ovarian follicular development in laying broiler breeders and commercial egg producing hens. Br. Poult. Sci. 19: 387-395.

Yoo, B.H., B.L. Sheldon, and R.N. Podger, 1986. Analyses of oviposition times and intervals in a wide range of layer flocks under normal and continuous lighting regimes. Br. Poult. Sci. 27: 267-288.

Yu, M.W., F.E. Robinson, R.G. Charles, and R. Weingardt, 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. Poultry Sci. 71: 1750-1761.

Yu, M.W., F.E. Robinson, M.T. Clandinin, and L. Bodnar, 1990. Growth and body composition of broiler chickens in response to different regimens of feed restriction. Poultry Sci. 69: 2074-2081.

Zakaria, A.H., T. Miyaki, and K. Imai, 1984. The relationship of clutch length and egg position on ovarian follicular growth in laying hens. Poultry Sci. 63: 1250-1254.

III. OVARIAN MORPHOLOGY AND CARCASS TRAITS AT SEXUAL MATURITY IN TWO STRAINS OF EGG-TYPE PULLETS PHOTOSTIMULATED WITH VARIOUS LIGHT INTENSITIES

III.1 INTRODUCTION

Breeders of Single Comb White Leghorn (SCWL) chickens have developed highly efficient strains through selection for age at sexual maturity, peak egg production, persistency of lay, feed efficiency, viability and disease resistance, fertility, hatchability, egg weight, albumen and shell quality, and the incidence of meat or blood spots. The evidence of genetic progress in egg-type chickens is well known and has been previously reported (Fairfull and Gowe, 1990; Hunton, 1990). Selection pressure to improve feed efficiency in SCWL has resulted in decreased mature BW (Hunton, 1990). Early sexual maturity reduces egg size (Harrison *et al.*, 1969; Bell *et al.*, 1982), partly as a result of decreased BW at sexual maturity (Summers and Leeson, 1983).

Exposing chickens to increasing day-lengths is known to stimulate sexual maturation (Morris, 1994). Photoschedule manipulation has become a standard industry procedure to influence flock age at onset of lay, rate of egg production, egg size, and feed efficiency (Etches, 1996). Lupicki (1994) observed a delay of 6.2 d for the onset of egg production in modern Leghorns housed under a constant 8L:16D photoschedule compared to pullets that were exposed to 14L:10D photoschedule at 20 wk of age. Eitan and Soller (1991) reported that supplemental light was not required for the onset of sexual maturity, although it had a significant effect on weight and age at first egg. Robinson *et al.* (1996b) also reported that late photostimulation delayed the onset of lay in SCWL. With increased age of photostimulation, the response time to first oviposition decreased and evidence of ovary and oviduct development was observed prior to the day-length increase.

The possibility that light intensity affects laying hens has been considered for many years and studies have been performed to identify the minimum light intensity required to induce a normal photoperiodic response in chickens. Dorminey *et al.* (1970) reviewed early

experimentation by Roberts and Carver (1941), Nicholas *et al.* (1944), Dobie *et al.* (1946) and Ostrander *et al.* (1960) which found no egg production response to various light intensities ranging from 5 to over 400 lux (1 footcandle = 10.76 lux). Light intensities of 16.1 and 32.2 lux did not alter fertility in turkey hens (McCartney, 1971), and intensities ranging from 2.2 to 10.8 lux did not affect fertility in naturally-mated, caged White Leghorns (Hughes, 1973).

Other experimental results have demonstrated that light intensity can affect reproductive traits. Wilson *et al.* (1956) reported that light intensities below 4 lux retarded sexual maturation in caged pullets. Dorminey *et al.* (1970) reported that sexual maturity was delayed by 1 wk in pullets reared under 8 h of 1.1 lux (measured 15 cm above the pen floor) compared to pullets reared under 3.2, 5.4, 10.8 and 32.3 lux, and about 2 wk later than pullets reared under subdued natural light with longer day-lengths. However, light intensity had no effect on hen-day egg production, egg weight or feed efficiency. King (1962) demonstrated that pullets reared in almost complete darkness eventually became sexually mature, but produced eggs at a lower rate (59%) than those hens raised on 6 h of 5-8 lux light with weekly day-length increases of 15 min (73% average annual production).

Morris and Owen (1966) reported a logarithmic linear decline in egg production when light intensity decreased from 10 to 0.08 lux. They concluded that the minimum light intensity for maximum egg production was more than 2 but less than 10 lux, and that 0.08 lux was equivalent to darkness for photoperiodic purposes. Morris and Bhatti (1978) concluded that the light intensity of the photophase must be at least ten times greater than intensity of the scotophase for chickens to normally entrain oviposition rhythms. Meyer *et al.* (1988) found that sexual development and activity of Japanese quail were dependent on photophase contrast rather than absolute light intensity. In this study, dim light was interpreted as darkness when brighter light was present, but was interpreted as day when the scotophase was completely dark. They also concluded that a bird's photoperiodic history did not influence whether or not it would be photostimulated with dim light. Morris (1967) demonstrated a dose response increase in egg production for hens in three-tiered cages with light intensities measured at the

middle tier food trough of 0.2, 1 and 5 lux, but no further increase in egg production under 25 lux. The relationship between light intensity (0.12 to 37 lux) and egg production to 500 d of age has further been estimated by Morris as $232.4 + 15.18X - 4.256X^2$ where X is the common logarithm of light intensity in lux (Curtis, 1981).

In more recent studies using caged laying hens, no significant differences in egg production were observed with light intensity ranging from 2 to 45 lux (Hill *et al.*, 1988). Similarly, Tucker and Charles (1993) found no consistent response to light intensities from 0.5 to 15 lux, which led these authors to suggest that modern prolific hybrid laying hens may be more tolerant of low light intensities than earlier stocks. Morris (1994) concluded that the laying strains of the 1980s are less sensitive to light than those of the 1960s. Dorminey *et al.* (1970) made reference to unpublished observations which indicate that breeds may differ in their response to low light intensity. Hill *et al.* (1988) suggested that the range of intensities utilized may not have been extreme enough to produce a clear response. In a recent study at the University of Alberta using broiler breeders, no difference in sexual development was found between hens photostimulated with either 10 or 100 lux (Muller *et al.* 1996).

The light intensity threshold in chickens for the onset of reproductive function appears to be relatively low. For this reason it has been suggested that management practices supply sufficient light intensity for safe working conditions and proper inspection of stock, rather than attempt to meet the chicken's minimum physiological requirement (Morris, 1994). The results of light intensity studies using large pens are also subject to question because the degree of illumination varies considerably with proximity to the light source. Measurements of light intensity in rearing pens (4.75 x 5.85 m) varied from 1 lux in the corners to 15 lux at floor level directly beneath the single hanging incandescent light bulb (H. Oosterhoff, unpublished data).

Although data is available examining the effect of light intensity on age at sexual maturity and egg production, few published data exist examining the effect of light intensity on reproductive morphology in chickens. The objective of this research was to investigate the

effects of light intensity on ovarian morphology, and compare differences in response to light intensity at photostimulation between a modern commercial strain of SCWL and an "antique" random-bred control strain.

III.2 MATERIALS AND METHODS

III.2.1 Stocks

A total of 32 commercial strain pullets (COMM, Shaver[1] Starcross 288) and 32 random-bred antique stock pullets (RBAS) closest to the flock mean BW were selected from a flock of Single Comb White Leghorns (SCWL) reared at the University of Alberta Poultry Research Centre[2]. The pullets were reared in floor pens under standard industry guidelines provided by Shaver Poultry Breeding Farms Ltd[1].

The RBAS strain flock has been maintained at the University of Alberta Poultry Research Center within its poultry genetics conservancy program. This strain originated from Kimber Farms, Inc., California, and was imported to Canada by S.S. Munro of Agriculture Canada around 1950 (R.D. Crawford, 1996, University of Saskatchewan, Saskatoon, Canada, S7N 0W0, personal communication). It was distributed as a genetic resource to Canadian experimental farms and universities, and became commonly known as the Saskatchewan Strain White Leghorn (R.D. Crawford, 1996, University of Saskatchewan , Saskatoon, Canada, S7N 0W0, personal communication). In 1974, R.D. Crawford of the University of Saskatchewan acquired control of a foundation flock consisting of 20 males and 60 females. Crawford (1990) has previously described the procedures used in maintaining this strain which included non-pedigreed natural mating in floor pens until 1985, and pedigreed random mating in caged flocks by artificial insemination from 1986 to 1990. The RBAS strain of SCWL was obtained by the University of Alberta from the University of Saskatchewan in 1990, and is currently being maintained under non-pedigreed random natural mating in floor pens as described for

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[1] Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

[2] University of Alberta, Edmonton, Alberta, Canada, T6G 2P5

the period prior to 1985. About 200 chicks are hatched for each yearly generation and reared under routine procedures. Females are chosen at random and rejected only on the basis of gross defects. Seventy hens are housed in two floor pens of 35 birds each, with three groups of five males rotating between a bachelor pen and the two pens of females. Hen-day production of the 1995 University of Alberta flock are illustrated in Figure I-1 alongside the performance objectives for the COMM strain (Anonymous, 1992).

III.2.2 Management and Experimental Design

Two hundred pullets of each strain were reared in 2 floor pens (4.75 x 5.85 m) in a light-tight facility under a photoschedule of 8L:16D. Light was supplied by a single incandescent light bulb per pen which provided a intensity of 1 to 15 lux at 30 cm from the floor, depending on the proximity to the light source. Beak trimming and comb dubbing were performed at 7 d of age. Fresh water and age appropriate rations were provided *ad libitum* throughout rearing and the experimental period. All experimental procedures performed on live birds were within the principles and guidelines approved by the University of Alberta, Faculty of Agriculture, Forestry and Home Economics, Animal Policy and Welfare Committee.

At 17 wk of age, 32 pullets of each strain were individually wing-banded, weighed and randomly placed in individual laying cages alternating by strain. Cages were constructed in batteries of 16 cages and each cage was illuminated by a dimmable overhead incandescent bulb. Light intensity for each group of battery cages was set to provide one of four light intensities at the feeder level: 1, 5, 50 or 500 lux. Light intensity was measured using a Li-Cor Quantum/Radiometer/Photometer (Model LI-188; Licor Inc, Lincoln, NE) which perceives light with a similar spectral intensity as the human eye. Reception of light energy occurs over the visible spectrum between wavelengths of 400 nm (blue light) and 700 nm (red light), with a maximum at a wavelength of 555 nm (green light). Feed was provided in individual containers to allow consumption to be recorded for each pullet. The cages were placed in a

large room which was divided into four quadrants by an opaque black curtain. The curtain was constructed to prevent all light transfer between quadrants without restricting adequate ventilation. Each quadrant contained one battery of cages, housing eight pullets of each strain, and was randomly assigned to one of the four light intensity treatments in a 2 x 4 factorial design (strain x light intensity, respectively).

At 18.6 wk, all pullets were photostimulated with an initial increase in day-length to 12L:12D within their respective light treatment. A step-up photoschedule was subsequently used with weekly light period increases of 30 min to a maximum day-length of 14L:10D at 22 wk. The pullets were blood sampled by brachial venipuncture (10 ml) prior to photostimulation at 18 wk and again at 20 wk of age. Individual BW and feed consumption data were recorded on a weekly basis. A blood sample was again collected from each of the 64 birds on the day of first oviposition and feed was withdrawn overnight (12-20 h) to facilitate gut clearance. The weight of the first egg was recorded for each hen and each egg collected was broken open to count the number of yolks it contained.

III.2.3 Carcass Examination

Each pullet was killed by cervical dislocation the day following first oviposition and the fasted intact carcass was weighed. Left shank length was measured (length of the tibiotarsus from the top of the hock joint to middle of the footpad) and recorded as an indicator of frame size. The birds were dissected and examined for carcass tissue traits. The weights of the abdominal fat pad including the fat surrounding the gizzard, breast muscle (*pectoralis major* and *minor*), liver, oviduct, ovary and stroma were recorded. The stroma weight comprised of the ovarian tissue remaining after the large yellow follicles (LYF) greater than 10 mm in diameter were removed. These component weights have been expressed on an actual organ weight basis and as a percentage of the fasted BW at processing. The LYF were counted and individually weighed. The number of small yellow follicles (SYF; 5 - 10 mm diameter) and post-ovulatory follicles (POF) were also counted. The birds were inspected for

traits which indicate the birds state of reproductive health, such as the incidence of internal ovulation, internal oviposition, ovarian regression, and follicular atresia.

The presence of a follicle or developing egg in the oviduct was recorded and stage of egg formation was estimated. Egg yolks were counted and if it was determined to result from an ovulation of the present day, it was extracted, weighed and used as the F1 follicle for calculating the corrected total and corrected average follicle weight. If it was determined that the bird had not yet ovulated that day, the largest follicle remaining on the ovary was specified as the F1. If a developing egg was found in the oviduct, it was considered to have been ovulated the same day if it had not yet entered the shell gland. The number of post-ovulatory follicles on the day following first oviposition was reconciled to the number of recovered yolks which included those of the first egg and those present in the reproductive tract upon examination.

All carcass components, except for the liver and oviduct, were labelled and stored together at -20°C. Livers and oviducts were labelled and individually stored at -20°C for later analysis of total liver lipid and oviduct protein content. Individual whole body composition was determined for each bird following the procedure described by Yu *et al.* (1990). Each carcass was individually autoclaved for 3.5 h and homogenized using an industrial pressure-cooker and blender. A 500 ml subsample of each homogenized carcass was freeze-dried and subjected to proximate analysis in duplicate for dry matter, ash, crude protein, and petroleum ether-extractable lipid content (Association of Official Analytical Chemists, 1980). The livers and oviducts were freeze-dried and ground in a blender. Total liver lipid content was determined by petroleum ether extraction. Oviduct samples were analyzed for crude protein. For each tissue analysis, a 2% difference between duplicates was accepted, with the exception of a 5% difference allowable for carcass ash content duplicates. Re-analysis was performed on carcass samples not meeting these criteria. Insufficient tissue was available to completely re-analyze a few liver and oviduct duplicates where differences exceeded 2%. In these cases, a third subsample was analyzed and the two results with least difference were averaged.

Blood samples were centrifuged at 2500 RPM for 11 min at 4°C and the plasma was stored at -20°C in individually labelled vials. Plasma estradiol-17β concentration was determined by using an antibody-coated tube, competitive-binding RIA[3]. Estradiol-17β concentrations in different volumes of a plasma sample were measured to determine parallelism (vol: mean ± SEM; 50 µl: 31 ± 3.0 pg/ml; 100 µl: 101.8 ± 6.8 pg/ml; 200 µl: 247.6 ± 8.4 pg/ml; 400 µl: 599.5 ± 14.0 pg/ml). Duplicate 200 µl samples of plasma were assayed with the controls indicating an intra-assay coefficient of variation of 8.35% and an inter-assay coefficient of variation of 4.09%. The RIA detection limit was approximately 8 pg/ml and the antiserum was highly specific for estradiol-17β as stated by the manufacturer. With the exception of estrone (10.0%), *d*-Equilenin (4.4%), estrone-β-D-glucuronide (1.8%) and ethinyl estradiol (1.8%), all other naturally occurring steroids or therapeutic drugs tested had a cross reactivity less than 1%. Duplicate 1.5 ml samples of plasma were sonicated prior to analysis of quantitative lipid content by chloroform-methanol method.

III.2.4 Statistical Analysis

The experiment was analyzed as a 2 x 4 factorial design. Sources of variation were strain (s = 2), light intensity (l = 4) and strain x light intensity. Error variation was considered to be birds within strain by light intensity. All data were analyzed by two-way ANOVA using the General Linear Models (GLM) procedures of SAS® software (SAS Institute, 1992). When significant differences were determined for light intensity or strain x light intensity, comparison among means were made using the Least Significant Difference (LSD) procedure. All statements of significance were assessed using $P < 0.05$.

III.3 RESULTS AND DISCUSSION

III.3.1 Strain Effects

Age of first oviposition was significantly different between the two strains. When

[3]Kit Number TKE25, Diagnostic Products Corp., Los Angeles, CA 90045-5597

pullets were photostimulated at 130 d of age, the average age of first oviposition was 155.9 d for the RBAS strain and 146.8 d for the COMM strain (Table III-1). The 9.1 d difference in age of sexual maturity represented a 35.1 % decrease in response time to photostimulation in the COMM strain compared to RBAS. The response time to photostimulation for the COMM strain was similar to that observed in the later maturing commercial (LM) strain of the previous experiment (Table II-3). The RBAS strain pullets were also less uniform in their response, as only 62.5% of the flock reached sexual maturity within ± 5% of the mean age of first oviposition, while 96.9% of the COMM strain were within this range. This provides evidence of reduced variation caused by selection and breeding programs in present-day commercial strains of SCWL.

At 18 wk of age, the BW of the COMM strain was significantly higher than the RBAS strain (Table III-2). However, this difference was not evident at first oviposition as the fasted BW in the COMM strain became numerically lower at this time (RBAS, 1416 g; COMM, 1370 g; Table III-2) and neared significance ($p = 0.055$). During the time period from photostimulation to first oviposition, the RBAS strain had a larger increase in BW than the COMM strain. This resulted from the increased age of sexual maturity in the RBAS strain, and was not a result of increased growth rate. In fact, the COMM strain achieved a higher rate of BW gain than the RBAS strain (RBAS, 12.9 g/d; COMM, 15.0 g/d; Table III-2), but a smaller total BW gain because of the shorter time required for sexual maturation to occur. These results would suggest support for the literature indicating a threshold BW is required for the onset of sexual maturity (Brody *et al.*, 1980, 1984; Soller *et al.*, 1984) as sexual maturity in the RBAS strain was delayed until it reached a common BW with the COMM strain. Body weight at sexual maturity was similar to that achieved by commercial strains of SCWL in the previous experiment (Table II-3), and slightly higher numerically than values reported by Robinson *et al.* (1996b) for SCWL. Shank length, an indicator of frame size, was observed to be similar between the two strains (Table III-2).

Abdominal fat pad weight was heavier in the RBAS strain than the COMM strain at

sexual maturity on both an absolute basis (RBAS, 42.2 g; COMM, 26.4 g, Table III-3), and expressed relative to BW (RBAS, 2.95%; COMM, 1.92%, Table III-3). These relative weights are similar to the values reported by Robinson *et al.* (1996b) of 2.5, 1.7 and 1.9% in pullets photostimulated at 16, 18, and 20 wk, respectively, although significant differences were not found by those authors. The differences between strains in fat pad weight at sexual maturity indicates that either the delayed sexual maturity in the RBAS strain was not limited by a lipid content threshold as proposed by Bornstein *et al.* (1984), or the lipid content threshold has significantly been reduced in the COMM strain by genetic selection for earlier sexual maturity and feed efficiency.

On an absolute weight basis, there was no difference in breast muscle (Table III-4), liver (Table III-5), ovary (Table III-6), or stroma weight (Table III-7) between strains. However, because of the higher BW of the RBAS strain at sexual maturity, the weights of the breast muscle, and ovary were lower when expressed relative to BW in the RBAS strain than the COMM strain.

There was no difference in number of SYF or LYF between strains at sexual maturity (Table III-8). However, the number of POF was different, both in numbers and those reconcilable to visible egg yolks (Table III-9). The RBAS strain showed both a higher number of POF (RBAS, 3.19; COMM, 2.63), and a higher number of irreconcilable POF (RBAS, 1.16; COMM, 0.09). The number of POF found in the COMM strain was similar to that occurring in the two commercial strains of SCWL in the previous experiment (Table II-3). A quantity of 2.5 POF's is understandable as most pullets had laid a second egg prior to being killed on the day following first oviposition, while approximately half had ovulated a third time as evidenced by a follicle in the oviduct. Post-ovulatory follicles that are not reconcilable with egg yolks at sexual maturity provide a numeric indication of internal ovulation, and this was confirmed by examination of the body cavity for the presence of yolky material. Renema *et al.* (1995) and Melnychuk *et al.* (1997) have previously observed that a high incidence of irreconcilable POF at sexual maturity contributed to reproductive

inefficiency in turkey hens. Internal ovulation at sexual maturity has been proposed to result from a lack of synchrony between the maturation of the oviduct and the ovary (Robinson *et al.*, 1996a; Melnychuk *et al.*, 1997).

Normally, the first oviposition follows the first ovulation by approximately 24 h or the time required for complete egg formation. However, if the infundibulum and oviduct are insufficiently mature to capture the first ovulation, the follicle drops into the body cavity and internal ovulation is said to occur. Further evidence that this occurred was provided by the lower weight oviducts found in the RBAS strain than the COMM strain (Table III-10), both on an absolute weight (RBAS, 42.8 g; COMM, 47.1 g), and relative to BW (RBAS, 3.02 %; COMM, 3.44 %). When internal ovulation occurs, first oviposition does not accurately represent the age when the pullet has first ovulated. For the RBAS strain, the age of first ovulation was probably 2 - 3 days prior to the age of first oviposition because of the high incidence of internal ovulation which occurred (1.16 irreconcilable POF). Internal ovulation also provides the explanation of higher numbers of POF found in the RBAS strain, as pullets killed at first oviposition had previously ovulated without producing an egg.

The total LYF weight (ovary weight - stroma weight) and average LYF weight were higher in the COMM strain as opposed to RBAS, whether or not the LYF weight was corrected for the weight of any F1 follicle in the oviduct (Table III-11). The higher LYF weight of the COMM strain was also apparent when LYF weight was expressed as a percent of BW, fat pad, and liver weight (Table III-12). Therefore, although number of LYF did not differ, the size of each LYF was larger in the modern COMM strain. This was further evidenced by the heavier corrected F1 follicle weight (RBAS, 7.4 g; COMM, 8.7 g) and initial egg weight (RBAS, 37.0 g; COMM 42.6 g) observed in the COMM strain than the RBAS strain (Table III-13).

Results of proximate analysis indicated a higher percentage of carcass lipid and a lower percentage of carcass moisture, protein and ash content in the RBAS strain compared to the COMM strain (Table III-14). On a weight basis, there was no difference between strains

for water and ash composition, although the RBAS strain had a lower protein weight (RBAS, 287.9 g; COMM, 303.2 g) and a greater lipid weight (RBAS, 225.3 g, COMM, 159.1 g) than the COMM strain (Table III-15). Analysis of individual livers for lipid content (Table III-16) produced results similar to those found in carcass lipid; the RBAS strain showed increased lipid content (%) and weight (g) as compared to the COMM strain. Results from oviducts analyzed for protein content were higher for the COMM strain (RBAS, 81.79 % DM, COMM, 83.40 % DM), although oviducts of the RBAS strain were higher in dry matter content (Table III-17).

Plasma estradiol-17β content between strains was similar prior to photostimulation at 18 wk of age. However, although both strains increased following photostimulation, the estradiol levels were higher in the RBAS strain at 20 wk of age (RBAS, 239.7 pg/ml; COMM, 166.0 pg/ml) and at first oviposition (RBAS, 189.3 pg/ml; COMM, 100.6 pg/ml, Table III-18). Plasma lipid content was different between the strains only in those samples collected on the day of first oviposition (RBAS, 6.11%; COMM, 3.50%, Table III-19).

Feed consumption data indicated that the RBAS strain consumed a greater amount of feed between photostimulation and first oviposition (Table III-20). This was a result of both the increased time to reach sexual maturity, as well as higher feed consumption per day (RBAS, 91.3 g; COMM, 85.3 g). The BW gain per day was lower in the RBAS strain as compared to the COMM strain, and feed efficiency (measured in terms of growth rather than egg production) was greatest in the COMM strain (RBAS, 14.11 %; COMM, 17.62 %). If a threshold BW is required for the onset of reproductive function as previously discussed, pullets would be required to grow at a faster rate in order to reach sexual maturity at younger ages. These data are evidence of selection pressure for both reduced age of first oviposition and feed efficiency of growth in modern strains of SCWL.

III.3.2 Effect of Light Intensity

There was no difference in the effect of light intensity on average age of first

oviposition across strains (Table III-1). These results differ from observations of Wilson *et al.* (1956) and Dorminey *et al.* (1970) that light intensities of 4 lux and 1.1 lux (respectively) delayed sexual maturity. The results of the present experiment may differ because a step-up lighting schedule was used, which provides a lengthening day signal each week. This photoschedule may have compensated for any decreased photostimulatory effect by the lowest light intensities. However, a slight increase in variability of age at first oviposition was noticed for the lower light intensities used in this study. The ratio of birds reaching sexual maturity within ±5 % of mean age for each light intensity (1 lux, 75.0 %; 5 lux, 43.8 %; 50 lux, 87.5 %; 500 lux, 87.5 %, Table III-1) may suggest that pullets receive a more distinct photostimulatory cue with increased light intensity and therefore produce a more uniform response to photostimulation.

Light intensity had no affect on pullet BW, shank length (Table III-2), absolute breast muscle (Table III-4), oviduct (Table III-10), and stroma weight (Table III-7). Breast muscle and stroma weight expressed relative to BW were not different between light intensities. The pullets photostimulated with 1 and 500 lux had larger abdominal fat pad and liver weights (expressed both in absolute terms and relative to BW) when compared to the birds in the intermediate light intensities of 5 and 50 lux (Table III-3, III-5). This possibly may result from decreased pullet activity under the lower light intensity and increased lipogenesis in the highest.

Ovary weight (Table III-6) expressed in both absolute terms and relative to BW, and relative oviduct weight (Table III-10) increased numerically in response to each logarithmic increase in light intensity at photostimulation, with a significant difference evident between 1 and 500 lux. These differences in ovary and oviduct development expressed relative to BW illustrate that a low light intensity of 1 lux does not produce as great a response in reproductive development as higher light intensities.

The quantity of LYF exhibited an increasing dose response to light intensity (1 lux, 5.50; 5 lux, 6.56; 50 lux, 7.31; 500 lux, 7.50; Table III-8), similar to that seen in oviduct and

ovary weight (Table III-10, III-6). A similar response was also observed in the total and corrected LYF weight expressed in absolute terms (Table III-11), as well as total LYF weight expressed relative to BW, fat pad weight and liver weight (Table III-12). The number of SYF was not different between light intensities (Table III-8). Average follicle weight (uncorrected) was not significantly different between light intensity treatments (Table III-11). This evidence would indicate that the greater ovary weight observed with increased light intensity was the primary result of increased LYF quantity and not an increase in their size. Further evidence that individual follicle weight did not contribute to increased ovary weight was provided by the lack of difference between the light treatments for the weights of F1 follicles (corrected) and first eggs (Table III-13). The reduced quantity of LYF under low light intensities suggests agreement with previous observations of reduced egg production under very low light intensities (Morris and Owen, 1966; Morris, 1967). These observations appear to disagree with Dorminey *et al.* (1970), Hill *et al.* (1988) and Tucker and Charles (1993), which reported no difference in egg production as a result of light intensities ranging from 1.1 to 34 lux. However, Hill *et al.* (1988) suggested that the range of intensities utilized may not have been extreme enough to produce a clear response. Although the results of the current experiment demonstrate a dose response to light intensity in the quantity of LYF, significant differences become evident only between the light intensity extremes.

Internal ovulation, as evidenced by the quantity of irreconcilable POF, exhibited an inverse relationship with light intensity. The quantity of irreconcilable POF (1.06) was highest in the pullets photostimulated with one lux of light intensity and decreased as light intensity increased (Table III-9). As previously discussed, internal ovulation may be the result of an immature oviduct being unable to capture the first ovulated follicles. It is apparent that light intensity has an effect on the development and growth of the oviduct, as well as recruitment into the hierarchy of LYF. The decreased oviduct weight observed with the 1 lux light intensity would provide further support for this explanation.

Light intensity affected pullet carcass composition. The highest percentage of carcass

lipid and the lowest percentage of carcass protein were found in pullets photostimulated with 1 lux (Table III-14). Carcass lipid weight, expressed in absolute terms, was highest under 1 lux, with no difference between 5, 50, and 500 lux (Table III-15). Lipid content of the liver was highest in birds photostimulated with 1 lux, lowest with 5 lux, and then increased as light intensity increased to 500 lux. This trend was evident when liver lipid was expressed in terms of both absolute weight and as a percent of liver dry matter (Table III-16). It is possible that the lowest light intensity reduced bird activity and decreased maintenance levels of energy required and permitted a greater proportion of energy to be allocated to lipid depots while increasing light intensity above 5 lux increased lipid lipogenesis by the liver.

As previously discussed, increases in light intensity stimulated the pullets to allocate more lipid to the ovary in terms of total ovary weight and increases in follicular recruitment into the LYF hierarchy. Although bird behaviour was not measured, it is likely that the higher carcass and liver lipid contents observed at 1 lux light intensity are the result of a reduction in bird activity without a decrease in feed consumption (Table III-20). The observation of greater abdominal fat pad weights in pullets photostimulated with 1 lux light intensity further supports the conclusion that a higher proportion of dietary energy was allocated to carcass deposits in these birds. Five lux appears to be sufficient for normal bird metabolism and the slight increases in carcass lipid with higher light intensities may well be the result of increased lipogenesis for reproductive function. Pullets photostimulated with 5 and 50 lux of light intensity had the highest carcass moisture content when compared to pullets in 1 and 500 lux.

Protein analysis of individual oviducts revealed no differences between pullets from the various light intensities. However, a decrease in oviduct dry matter was observed as light intensity increased from 1 to 50 lux (Table III-17). This suggests that the decreased oviduct weight as a percent of BW in pullets from the 1 lux treatment is not simply a function of lean tissue growth. It is suggested that the ability of the infundibulum to capture the first ovulation may be related to oviduct maturity and motility rather than simply size. Interestingly, no differences were observed in plasma estradiol-17β (Table III-18) or plasma lipid content

(Table III-19) for any collection period as a result of light intensity treatment.

III.3.3 Interactions between main effects

The primary effects of strain and light intensity were generally sufficient to explain differences between observations. There were very few significant interactions between main effects. Significant interactions were observed in the values for stroma weight (Table III-7), number of SYF (Table III-8), and the concentration of plasma estradiol-17β prior to photostimulation at 18 wk (Table III-18). In these three parameters, the high values in the RBAS strain at 1 lux were not expected because these pullets generally appeared to be less responsive to low light intensity. One factor contributing to these results, however, was the higher incidence of internal ovulation in these pullets (Table III-9). The occurrence of internal ovulation was highest in the RBAS strain with low light intensities, and there were no internal ovulations observed in the COMM strain under either 50 or 500 lux. Since carcass examination was performed only after the first observed oviposition, the ovaries of the RBAS pullets under low light intensity were actually more mature by a few days than their counterparts because of the higher incidence of internal ovulation. The higher estradiol concentration prior to photostimulation in the RBAS pullets in 1 lux is consistent with higher SYF quantity and stroma weight because estradiol is known to be produced by the pool of small follicles (Robinson and Etches, 1986). Another possible explanation is that more variation exists within the RBAS strain.

The quantity of LYF (Table III-8) would appear to illustrate that increases in light intensity had a greater affect on the COMM strain than RBAS, although the interaction was not statistically significant. Tucker and Charles (1993) suggested that modern prolific hybrid laying hens may be more tolerant of low light intensities than earlier stocks. Morris (1994) suggested that laying strains of the 1980s were less sensitive to light intensity than those of the 1960s because recent studies with modern strains have not shown the same light intensity effects on rate of lay as earlier studies.

The data presented here demonstrates that a modern COMM strain of SCWL responds to photostimulation and reaches sexual maturity at an earlier age than the random-bred antique control strain. Modern commercial strains of SCWL are the product of strict genetic selection and breeding programs that have been successful at developing very reproductively efficient birds. These strains exhibit decreased age at first oviposition, and changes in reproductive morphology and response to light. Although the intensity of photostimulatory light did not affect age of first oviposition, an effect on reproductive organ morphology was observed in ovary and oviduct growth, and the quantity of LYF. Internal ovulation, as evidenced by irreconcilable POF, was reduced by increasing the intensity of photostimulatory light. Genetic selection for reproductive efficiency in modern strains appears to have greatly reduced the incidence of internal ovulation in SCWL at sexual maturity.

The modern SCWL appears to be stimulated by lower levels of light than its predecessors. This reduced light intensity threshold required for normal reproductive function suggests modern COMM strains are actually more sensitive to light. Even though very low light intensity (1 lux) is less likely to detrimentally affect modern strains of SCWL, the threshold level for a complete morphological response to photostimulation is between 5 and 50 lux. As light intensity increases above 5 lux, there is an increasing allocation of lipid to the developing follicles. Further study may be required to determine if even higher light intensities (>500 lux) will overstimulate lipogenesis in the modern pullet, leading to similar reproductive problems as found in overweight broiler breeder hens (Robinson *et al.*, 1991, 1993; Yu *et al.*, 1992).

If modern SCWL are able to respond to lower light levels, it becomes even more critical to rear pullets under management of strict light control. Momentary or minute light leaks into a light-tight housing environment need to be eliminated in order to prevent the ultra-sensitive modern strains from initiating sexual development at too early an age. Robinson *et al.* (1996b) has previously described the effect of early photostimulation on modern strain SCWL pullets. The knowledge that strain differences exist provides reason to examine

whether various modern strains of SCWL react differently to photostimulation at different ages as well. With the development of highly specific genetic strains, it will be increasingly important to match the environmental management practices to the particular strain of hens.

III-4 TABLES AND FIGURES

Table III-1. Age at first oviposition for two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Age at 1st Oviposition (d)	Duration from Photostimulation to 1st Oviposition (d)	Birds within ± 5% of Mean (%)
Strain					
	RBAS[1]	32	155.9[a]	25.9[a]	62.5
	COMM[2]	32	146.8[b]	16.8[b]	96.9
	SEM		1.3	1.3	
Light Intensity (lux)					
	1	16	152.7	22.7	75.0
	5	16	153.6	23.6	43.8
	50	16	149.4	19.4	87.5
	500	16	149.6	19.6	87.5
	SEM		1.8	1.8	

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-2. BW growth parameters and shank length in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	18 wk BW (g)	BW[1] at 1st Oviposition (g)	Rate[2] of BW Gain (g/d)	Shank Length (mm)
Strain						
	RBAS[3]	32	1183[b]	1416	12.9[b]	98.4
	COMM[4]	32	1217[a]	1370	15.0[a]	98.8
	SEM		11	17	0.6	0.4
Light Intensity (lux)						
	1	16	1199	1415	14.1	98.1
	5	16	1185	1377	12.6	98.5
	50	16	1213	1390	14.6	99.5
	500	16	1204	1391	14.3	98.5
	SEM		16	24	0.9	0.6

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] BW recorded after fasting on day following 1st Oviposition

[2] Calculated from: (BW on day of 1st oviposition - 18 wk BW) / Duration from Photostimulation to 1st Oviposition

[3] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[4] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-3. Abdominal fat pad weight on an absolute basis and relative to BW at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	Fat Pad Weight (g)	Fat Pad Weight Relative to BW (%)
Strain			
RBAS[1]	32	42.2[a]	2.95[a]
COMM[2]	32	26.4[b]	1.92[b]
SEM		2.1	0.14
Light Intensity (lux)			
1	16	42.0[a]	2.93[a]
5	16	30.7[b]	2.21[b]
50	16	30.4[b]	2.17[b]
500	16	34.1[ab]	2.43[ab]
SEM		3.0	0.19

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-4. Breast muscle weight on an absolute basis and relative to BW at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	Breast Muscle Weight (g)	Breast Muscle Weight relative to BW (%)
Strain			
RBAS[1]	32	188.4	13.35[b]
COMM[2]	32	195.3	14.27[a]
SEM		2.9	0.20
Light Intensity (lux)			
1	16	197.8	14.00
5	16	190.0	13.88
50	16	192.1	13.85
500	16	187.6	13.51
SEM		4.1	0.28

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-5. Liver weight on an absolute basis and relative to BW at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Liver Weight (g)	Liver Weight relative to BW (%)
Strain				
	RBAS[1]	32	26.4	1.87
	COMM[2]	32	24.3	1.77
	SEM		0.8	0.05
Light Intensity (lux)				
	1	16	27.3^{a}	1.94^{a}
	5	16	22.6^{b}	1.64^{b}
	50	16	24.9^{ab}	1.79^{ab}
	500	16	26.6^{a}	1.91^{a}
	SEM		1.1	0.08

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-6. Ovary weight on an absolute basis and relative to BW at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Ovary Weight (g)	Ovary Weight relative to BW (%)
Strain				
	RBAS[1]	32	30.7	2.15[b]
	COMM[2]	32	35.5	2.59[a]
	SEM		1.8	0.12
Light Intensity (lux)				
	1	16	26.9[b]	1.87[b]
	5	16	31.9[ab]	2.32[ab]
	50	16	36.1[a]	2.59[a]
	500	16	37.4[a]	2.70[a]
	SEM		2.6	0.17

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-7. Ovarian stroma weight on an absolute basis and relative to BW at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	Stroma weight (g)	Stroma weight relative to BW (%)
Strain			
RBAS[1]	32	3.92	0.28
COMM[2]	32	3.54	0.26
SEM		0.19	0.01
Light Intensity (lux)			
1	16	3.37	0.24
5	16	3.60	0.26
50	16	3.91	0.28
500	16	4.04	0.29
SEM		0.30	0.02
Strain * Light Intensity (lux) Interaction			
RBAS * 1	8	4.25[a]	0.29[a]
RBAS * 5	8	3.44[ab]	0.24[ab]
RBAS * 50	8	3.91[a]	0.27[a]
RBAS * 500	8	4.07[a]	0.29[a]
COMM * 1	8	2.49[b]	0.18[b]
COMM * 5	8	3.75[a]	0.28[a]
COMM * 50	8	3.91[a]	0.29[a]
COMM * 500	8	4.01[a]	0.29[a]
SEM		0.38	0.02

[a,b] For each main effect or the interaction, means within a column with no common superscript differ significantly ($P < 0.05$).
[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5
[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-8. Number of small yellow follicles (SYF) and large yellow follicles (LYF) at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	# of SYF	# of LYF
Strain			
RBAS[1]	32	3.91	6.56
COMM[2]	32	3.63	6.88
SEM		0.33	0.34
Light Intensity (lux)			
1	16	4.13	5.50^{b}
5	16	3.06	6.56^{ab}
50	16	4.56	7.31^{a}
500	16	3.31	7.50^{a}
SEM		0.46	0.48
Strain * Light Intensity (lux) Interaction			
RBAS * 1	8	5.63^{a}	6.13
RBAS * 5	8	2.75^{c}	6.50
RBAS * 50	8	4.25^{abc}	6.75
RBAS * 500	8	3.00^{c}	6.88
COMM * 1	8	2.63^{c}	4.88
COMM * 5	8	3.38^{bc}	6.63
COMM * 50	8	4.88^{ab}	7.88
COMM * 500	8	3.63^{bc}	8.13
SEM		0.65	0.68

[a,b,c] For each main effect or the interaction, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-9. Number of post-ovulatory follicles (POF), reconcilable and irreconcilable with egg yolks, at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	# of POF	# of POF reconcilable with egg yolks	# of irreconcilable POF
Strain				
RBAS[1]	32	3.19[a]	2.03[b]	1.16[a]
COMM[2]	32	2.63[b]	2.53[a]	0.09[b]
SEM		0.15	0.13	0.13
Light Intensity (lux)				
1	16	2.81	1.75[b]	1.06[a]
5	16	2.88	2.13[ab]	0.75[ab]
50	16	3.06	2.63[a]	0.44[b]
500	16	2.88	2.63[a]	0.25[b]
SEM		0.22	0.18	0.18
Strain * Light Intensity (lux) Interaction				
RBAS * 1	8	3.63[3]	1.63	2.00[3]
RBAS * 5	8	3.00	1.75	1.25
RBAS * 50	8	3.13	2.25	0.88
RBAS * 500	8	3.00	2.50	0.50
COMM * 1	8	2.00	1.88	0.13
COMM * 5	8	2.75	2.50	0.25
COMM * 50	8	3.00	3.00	0.00
COMM * 500	8	2.75	2.75	0.00
SEM		0.31	0.26	0.26

[a,b] For each main effect or the interaction, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

[3] Interaction neared significance $p<0.10$.

Table III-10. Oviduct weight on an absolute basis and relative to BW at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	Oviduct weight (g)	Oviduct weight relative to BW (%)
Strain			
RBAS[1]	32	42.8[b]	3.02[b]
COMM[2]	32	47.1[a]	3.44[a]
SEM		0.9	0.06
Light Intensity (lux)			
1	16	42.8	3.04[b]
5	16	44.8	3.26[a]
50	16	45.7	3.29[a]
500	16	46.3	3.33[a]
SEM		1.3	0.08

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).
[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5
[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-11. Parameters of large yellow follicle (LYF) weight at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Total LYF weight (g)	Average LYF weight (g)	Corrected[1] total LYF weight (g)	Corrected average LYF weight (g)
Strain						
	RBAS[2]	32	26.8[b]	4.12[b]	29.0[b]	4.43[b]
	COMM[3]	32	31.9[a]	4.64[a]	37.3[a]	5.27[a]
	SEM		1.7	0.15	1.9	0.16
Light Intensity (lux)						
	1	16	23.5[b]	4.24	25.3[b]	4.29[b]
	5	16	28.3[ab]	4.33	33.0[a]	5.02[a]
	50	16	32.2[a]	4.50	36.3[a]	5.00[a]
	500	16	33.4[a]	4.47	38.2[a]	5.08[a]
	SEM		2.4	0.21	2.62	0.22

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] A follicle collected from the oviduct resulting from a current day ovulation prior to death was designated the F1 and its weight added to LYF weight as a correction factor.

[2] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[3] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-12. Large yellow follicle (LYF) weight relative to carcass component weights at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	LYF weight relative to BW (%)	LYF weight relative to fat pad weight (%)	LYF weight relative to liver weight (%)
Strain					
	RBAS[1]	32	1.87[b]	71.6[b]	104.1[b]
	COMM[2]	32	2.33[a]	140.8[a]	133.3[a]
	SEM		0.12	10.1	7.2
Light Intensity (lux)					
	1	16	1.64[b]	65.8[b]	87.6[b]
	5	16	2.06[ab]	110.5[a]	124.2[a]
	50	16	2.31[a]	128.7[a]	131.6[a]
	500	16	2.41[a]	119.8[a]	131.4[a]
	SEM		0.16	14.3	10.2

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-13. Corrected[1] F1 follicle and initial egg weight at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Corrected F1 follicle weight (g)	First egg weight (g)
Strain				
	RBAS[2]	32	7.4[b]	37.0[b]
	COMM[3]	32	8.7[a]	42.6[a]
	SEM		0.3	1.0
Light Intensity (lux)				
	1	16	7.3	39.6
	5	16	8.0	41.2
	50	16	8.4	38.9
	500	16	8.4	39.4
	SEM		0.4	1.4

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] A follicle collected from the oviduct resulting from a current day ovulation prior to death was designated the F1.

[2] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[3] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-14. Carcass compositions of moisture, protein, lipid and ash (percent basis) at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Carcass moisture (%)	Carcass protein (%)	Carcass lipid (%)	Carcass ash (%)
Strain						
	RBAS[1]	32	56.3[b]	21.9[b]	16.9[a]	3.6[b]
	COMM[2]	32	58.4[a]	23.9[a]	12.5[b]	3.8[a]
	SEM		0.3	0.2	0.5	0.1
Light Intensity (lux)						
	1	16	56.8[bc]	22.2[b]	16.2[a]	3.4
	5	16	58.2[a]	23.2[a]	13.5[b]	3.8
	50	16	58.1[ab]	22.8[ab]	14.0[b]	3.8
	500	16	56.4[c]	23.4[a]	15.3[ab]	3.8
	SEM		0.5	0.3	0.7	0.1

[a,b,c] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-15. Carcass composition of moisture, protein, lipid and ash (weight basis) at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Carcass moisture weight (g)	Carcass protein weight (g)	Carcass lipid weight (g)	Carcass ash weight (g)
Strain						
	RBAS[1]	32	742.3	287.9[b]	225.3[a]	46.8
	COMM[2]	32	741.3	303.2[a]	159.1[b]	48.0
	SEM		8.4	3.1	8.0	1.0
Light Intensity (lux)						
	1	16	746.7	291.8	215.8[a]	44.9
	5	16	746.6	296.8	174.0[b]	48.1
	50	16	747.7	293.2	180.0[b]	48.4
	500	16	726.0	300.5	199.0[ab]	48.2
	SEM		11.9	4.4	11.4	1.3

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-16. Liver lipid and dry matter composition parameters at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Dried liver weight (g)	Liver DM (%)	Liver lipid (% DM)	Liver lipid weight (g)
Strain						
	RBAS[1]	32	16.98[a]	65.54	25.76[a]	4.84[a]
	COMM[2]	32	15.49[b]	63.92	18.34[b]	3.10[b]
	SEM		0.49	0.68	2.14	0.57
Light Intensity (lux)						
	1	16	17.77[a]	65.24	29.74[a]	5.83[a]
	5	16	14.68[c]	65.15	15.28[c]	2.28[c]
	50	16	15.51[bc]	62.40	17.68[bc]	2.90[bc]
	500	16	17.00[ab]	64.13	25.51[ab]	4.87[ab]
	SEM		0.70	0.96	3.03	0.81

[a,b,c] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-17. Oviduct protein and dry matter composition parameters at sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Dried oviduct weight (g)	Oviduct DM (%)	Oviduct protein (% DM)	Oviduct protein weight (g)
Strain						
	RBAS[1]	32	10.02	23.46[a]	81.79[b]	8.20
	COMM[2]	32	9.89	20.96[b]	83.40[a]	8.26
	SEM		0.27	0.33	0.36	0.24
Light Intensity (lux)						
	1	16	10.02	23.35[a]	82.55	8.30
	5	16	9.93	22.13[ab]	82.97	8.25
	50	16	9.85	21.61[b]	82.27	8.11
	500	16	10.01	21.76[b]	82.59	8.28
	SEM		0.37	0.47	0.51	0.34

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-18. Plasma estradiol-17β concentration at 18 wk, 20 wk, and sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment	n	18 wk plasma E-17β[1](pg/ml)	n	20 wk plasma E-17β (pg/ml)	n	1st egg plasma E-17β (pg/ml)
Strain						
RBAS[2]	32	67.0	30	239.7[a]	28	189.3[a]
COMM[3]	32	67.0	26	166.0[b]	26	100.6[a]
SEM		7.1		20.6		15.5
Light Intensity (lux)						
1	16	62.2	15	187.8	14	146.4
5	16	67.7	13	232.3	14	157.6
50	16	57.2	14	159.4	12	117.0
500	16	81.0	14	231.9	14	158.8
SEM		10.1		29.5		22.8
Strain * Light Intensity (lux) Interaction						
RBAS * 1	8	82.9[ab]	7	215.1	6	170.4
RBAS * 5	8	44.7[bc]	8	294.4	8	200.3
RBAS * 50	8	63.4[abc]	8	198.9	7	168.7
RBAS * 500	8	77.1[abc]	7	250.2	7	217.6
COMM * 1	8	41.5[c]	8	160.6	8	122.4
COMM * 5	8	90.7[a]	5	170.1	6	114.9
COMM * 50	8	51.0[abc]	6	119.9	5	65.2
COMM * 500	8	84.9[a]	7	213.5	7	100.1
SEM		14.2		46.3		34.8

[a,b,c] For each main effect or the interaction, means within a column with no common superscript differ significantly ($P < 0.05$). SEM listed for lowest n.

[1] E-17β = Estradiol-17β

[2] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[3] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-19. Plasma lipid concentration at 18 wk, 20 wk, and sexual maturity in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	18 wk plasma lipid (%)	n	20 wk plasma lipid (%)	n	1st egg plasma lipid (%)
Strain							
	RBAS[1]	32	0.63	30	4.52	29	6.11[a]
	COMM[2]	32	0.55	26	3.96	26	3.50[b]
	SEM		0.05		0.45		0.48
Light Intensity (lux)							
	1	16	0.64	15	4.23	15	5.79
	5	16	0.51	13	4.15	14	4.85
	50	16	0.61	14	3.71	12	3.98
	500	16	0.60	14	4.88	14	4.58
	SEM		0.07		0.64		0.70

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$). SEM listed for lowest n.

[1] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[2] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

Table III-20. Feed efficiency and growth characteristics from photostimulation to first oviposition in two strains of Single Comb White Leghorn pullets subjected to various light intensities of photostimulation

Treatment		n	Consumed feed from 18 wk to 1st Egg (g)	Rate of feed intake (g/d)	Rate of BW gain (g/d)	Feed efficiency of growth (%)
Strain						
	RBAS[2]	32	2342.5[a]	91.3[a]	12.9[b]	14.11[b]
	COMM[3]	32	1408.2[b]	85.3[b]	15.0[a]	17.62[a]
	SEM		111.4	1.9	0.6	0.69
Light Intensity (lux)						
	1	16	2026.3	88.7	14.1	16.12
	5	16	1948.8	82.6	12.6	15.52
	50	16	1797.0	92.4	14.6	15.90
	500	16	1729.3	89.4	14.3	15.92
	SEM		157.5	2.6	0.9	0.97

[a,b] For each main effect, means within a column with no common superscript differ significantly ($P < 0.05$).

[1] Calculated from: (BW on day of 1st oviposition - 18 wk BW) / Duration from Photostimulation to 1st Oviposition

[2] Random-bred antique stock, University of Alberta Poultry Research Centre, Edmonton, AB, Canada T6G 2P5

[3] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

III.5 REFERENCES CITED

Anonymous, 1992. Shaver Starcross 288 Commercial Management Guide, Shaver Poultry Breeding Farms Limited, Cambridge, Ontario, Canada N1R 5V9.

Association of Official Analytical Chemists, 1980. Official Methods of Analysis, 13th ed AOAC, Washington, D.C.

Bell, D.D., D.R. Kuney, and C.J. Adams, 1982. Varying the age of sexual stimulation in SCWL pullets. Poultry Sci. 61:1416 (Abstr.).

Bornstein, S., I. Plavnik, and Y. Lev, 1984. Body weight and/or fatness as potential determinants of the onset of egg production in broiler breeder hens. Br. Poult. Sci. 25: 323-341.

Brody, T., Y. Eitan, M. Soller, I. Nir, and Z. Nitsan. 1980. Compensatory growth and sexual maturity in broiler females reared under severe food restriction from day of hatching. Br. Poult. Sci. 21: 437-446.

Brody, T.B., P.B. Siegel, and J.A. Cherry, 1984. Age, body weight, and body composition requirements for the onset of sexual maturity of dwarf and normal chickens. Br. Poult. Sci. 25: 245-252.

Crawford, R.D., 1990. Experience with *in situ* preservation of poultry breeds. *in:* Animal Genetic Resources: A global programm for sustainable development. Proc. FAO Expert Consultation: Anim. Prod. Health Paper 80. pp 143-150.

Curtis, S.E., 1981. Environmental Management in Animal Agriculture. Animal Environment Services, Mahomet, IL.

Dobie, J.B., J.S. Carver, and J. Roberts, 1946. Poultry lighting for egg production. Washington Agri. Exper. Sta. Bull. No. 471.

Dorminey, R.W., J.E. Parker, and W.H. McClusky, 1970. Effect of light intensity on leghorn pullets during the development and laying periods. Poultry Sci. 49: 1657-1661.

Eitan, Y., and M. Soller, 1991. Two-way selection for threshold body weight at first egg in broiler strain females. 2. Effect of supplemental light on weight and age at first egg. Poultry Sci. 70: 2017-2022.

Etches, R.J., 1996. Reproduction in Poultry. CAB International. Wallingford, UK.

Fairfull, R.W., and R.S. Gowe, 1990. Genetics of egg production in chickens. pp 705-760. *in*: Poultry Breeding and Genetics. Developments in Animal and Veterinary Sciences, 22. Crawford, R.D., ed. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.

Harrison, P.C., G. Schmaier, and J. McGinnis, 1969. Reproductive development and response of White Leghorn pullets subjected to increasing daylengths at different ages. Poultry Sci. 48: 1021-1026.

Hill, J.A., D.R. Charles, H.H. Spechter, R.A. Bailey and A.J. Ballantyne, 1988. Effects of multiple environmental and nutritional factors on laying hens. Br. Poult. Sci 29: 499-511.

Hughes, B.L., 1973. Effect of light intensity on fertility of naturally-mated white leghorns. Poultry Sci. 52: 1968-1969.

Hunton, P., 1990. Industrial breeding and selection. pp 985-1028. *in*: Poultry Breeding and Genetics. Developments in Animal and Veterinary Sciences, 22. Crawford, R.D., ed. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.

King, D.F., 1962. Egg production of chickens raised and kept in darkness. Poultry Sci. 41: 1449.

Lupicki, M.E., 1994. Ovarian morphology and steroidogenesis in domestic fowl (*Gallus domesticus*): Effects of aging, strain, photostimulation program and level feeding. M.Sc. Thesis, University of Alberta, Edmonton, AB.

McCartney, M.G., 1971. Reproduction of turkeys as affected by age at lighting and light intensity. Poultry Sci. 50: 661-662.

Melnychuk, V.L., F.E. Robinson, R.A. Renema, R.T. Hardin, D.A. Emmerson, and L.G. Bagley, 1997. Carcass traits and reproductive development at the onset of lay in two lines of female turkeys. Poultry Sci. 76: 1197-1204.

Meyer, W.E., J.R. Millam, and F.A. Bradley, 1988. Photostimulation of Japanese quail by dim light depends upon photophase contrast, not light intensity. Biol. Reprod. 38:536-543.

Morris, T.R., 1967. The effect of light intensity on growing and laying pullets. Wld's Poultry Sci. J. 23: 246-252.

Morris, T.R., 1994. Lighting for layers: what we know and what we need to know. Wld's Poultry Sci. J. 50:283-287.

Morris, T.R., and B.M. Bhatti, 1978. Entrainment of oviposition in the fowl using bright and dim light cycles. Br. Poult. Sci. 19: 341-348.

Morris, T.R., and V.M. Owen, 1966. The effect of light intensity on egg production. Proc. 13th Wld's Poultry Congress, pp. 458-461.

Muller, L.D., F.E. Robinson, P.R. Goerzen, and J.J.R. Feddes, 1996. The effects of increasing day length and/or light intensity at 20 wk of age on sexual maturity in female broiler breeders. Poultry Sci. 75 (Suppl. 1): 57 (Abstr.).

Nicholas, J.E., E.W. Callenbach, and R.R. Murphy, 1944. Light intensity as a factor in the artificial illumination of pullets. Pennsylvania Agric. Exp. Sta. Bull. No. 462.

Ostrander, C.E., R.K. Ringer, H.C. Zindel and C.N. Turner, 1960. The effect of various light intensities on egg production of Single Comb White Leghorn pullets. Quart. Bull. Michigan St. Univ. Agric. Exper. Sta. 43: 292-297.

Renema, R.A., F.E. Robinson, V.L. Melnychuk, R.T. Hardin, L.G. Bagley, D.A. Emmerson and J.R. Blackman, 1995. The use of feed restriction for improving reproductive traits in male-line large white turkey hens. 2. Ovary morphology and laying trait characteristics. Poultry Sci. 73: 1724-1738.

Roberts, J., and J.S. Carver, 1941. Electric light for egg production. Agric. Engr. 22: 357-360, 364.

Robinson, F.E., and R.J. Etches, 1986. Ovarian steroidogenesis during follicular maturation in the domestic fowl (*Gallus domesticus*). Biol. Reprod. 35: 1096-1105.

Robinson, F.E., V.L. Melnychuk, L.D. Muller, H.H. Oosterhoff, T.A. Wautier and J.L. Wilson, 1996a. Sexual maturation in female domestic poultry as influenced by photostimulation program. pp. 110-122 *in:* Proceedings of 45th Annual National Breeders Round Table Meeting, St. Louis, MO, May 2-3, 1996.

Robinson, F.E., N.A. Robinson, and T.A. Scott, 1991. Reproductive performance, growth rate, and body composition of full-fed versus feed-restricted broiler breeder hens. Can. J. Anim. Sci. 71: 549-556.

Robinson, F.E., T.A. Wautier, R.T. Hardin, J.L. Wilson, M. Newcombe, and R.I. McKay, 1996b. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 2. Egg-type hens. Can. J. Anim. Sci. 76: 283-288.

Robinson, F.E., J.L. Wilson, M.W. Yu, G.M. Fasenko, and R.T. Hardin, 1993. The relationship between body weight and reproductive efficiency in meat-type chickens. Poultry Sci. 72: 912-922.

SAS Institute, 1992. The SAS® System for Windows 3.10. Release 6.08. Cary, N.C.

Soller, M., T. Brody, Y. Eitan, T. Agursky, and C. Wexler, 1984. Minimum weight for onset of sexual maturity in chickens: Heritability and phenotypic and genetic correlations with early growth rate. Poultry Sci. 63: 2103-2113.

Summers, J.D., and S. Leeson, 1983. Factors influencing early egg size. Poultry Sci. 62: 1155-1159.

Tucker, S.A., and D.R. Charles, 1993. Light intensity, intermittent lighting and feeding regimen during rearing as affecting egg production and egg quality. Br. Poult. Sci. 34: 255-266.

Wilson, W.O., A.E. Woodard, and H. Abplanalp, 1956. The effect and after-effect of varied exposure to light on chicken development. Biol. Bull. 111: 415-422.

Yu, M.W., F.E. Robinson, R.G. Charles, and R. Weingardt, 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. Poultry Sci. 71: 1750-1761.

Yu, M.W., F.E. Robinson, M.T. Clandinin, and L. Bodnar, 1990. Growth and body composition of broiler chickens in response to different regimens of feed restriction. Poultry Sci. 69: 2074-2081.

IV. CONCLUDING REMARKS

IV.1 INTRODUCTION

The Single Comb White Leghorn (SCWL) hen has developed into a highly efficient egg producer through many years of genetic selection and breeding. Targets for cumulative hen-housed egg production reach 280 eggs by about 68 wk of age (Anonymous, 1991; 1992), and it is relatively common for SCWL hens to lay greater than 300 eggs in an annual laying period. Selection for egg production is usually based either on the number of eggs to a fixed date (full or partial record), or on some calculated parameter such as rate of lay (Hunton, 1990). Rate of lay is often expressed as hen-day egg production which is calculated by dividing the number of eggs produced by the number of hens in the flock and expressing the result as a percentage (Etches, 1996). Hen-housed egg production provides a measure of the influence of mortality in a flock and is calculated by dividing the number of eggs by the number of hens in the flock upon commencement of lay. Both hen-day and hen-housed egg production are expressions of the mean oviposition rate for a flock, but they do not identify individuals or causes when production is poor. Flock rates of lay below the theoretical maximum of one egg per day per hen or 100% hen-day production may be caused by either a proportion of hens that are not laying while others are laying long sequences, or to shorter oviposition sequences by all hens (Etches, 1996). Therefore, rate of lay and cumulative egg production to a fixed date may not necessarily be the best selection criteria to identify hens with the greatest ability to lay one egg per day for extended periods of time.

IV.2 STRAIN DIFFERENCES

The results of these studies have confirmed that differences exist in mature BW, age at sexual maturity, ovarian morphology and egg production profiles between strains of SCWL. In the first experiment, hens of the early maturing (EM) strain[1] displayed increased proportional growth and development of reproductive organs and decreased proportional

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[1] Babcock B300, ISA Babcock, Division of ISA Breeders, Inc. P.O. Box 280, Ithaca, NY. 14851

carcass growth when compared with the later maturing (LM) strain[2]. In the second experiment, comparison between a modern commercial (COMM)[3] and a random-bred "antique" control strain (RBAS)[4] suggests that genetic selection has decreased internal ovulation through earlier oviduct development relative to the ovary. Since differences were observed between strains under similar management conditions, it is likely that the maximum production response for each strain may be found under different management programs.

As expected, the two strains of SCWL used in the first experiment differed in age at sexual maturity. The LM strain initiated lay later than the EM strain and achieved a greater mature BW, but total egg production to 68 wk was the same (EM: 296.5; LM: 298.8). The LM strain produced a greater quantity of normal shelled eggs than the EM strain because of the reduced incidence of gross shell defects. It is evident that there are genetic differences between hens which produce similar total number of eggs to 68 wk of age. Breeding programs and selection criteria which rely only on cumulative egg production do not identify individuals hens with the ability to produce at maximum production for long periods of time. Prime sequence length and average sequence length were significantly different between strains, even though total egg production was similar. It is suggested that selection on longer prime sequence or average sequence length may be an effective way to develop strains with the ability to maintain a high rate of lay for extended periods of time. The strong positive correlation between prime sequence length and normal egg production on a flock basis supports the use of prime sequence length as part of a multiple-trait genetic selection program.

Unfortunately, feed intake was not recorded in the first experiment. For this reason, no specific conclusions can be drawn in regards to a comparison of profitability or efficiency

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[2] Shaver White, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

[3] Shaver Starcross 288, Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9

[4] Saskatchewan Strain White Leghorn, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5

between strains. Similarly, the cause of increased cage layer fatigue and shorter sequences in the EM strain could not be conclusively attributed to decreased feed or nutrient intake. With similar egg production, the EM strain may be the most economically profitable strain if feed costs are proven to be substantially reduced. It is likely that feed intake was lower in the EM strain because lower BW birds are known to have a lower maintenance requirement. It is also possible that in the development of the EM strain, more emphasis was placed on feed efficiency than in the LM strain. The ability to lay one egg per day for extended periods of time appears to have been compromised in the lower body weight EM strain. This likely results from a combination of reduced body reserves and lower nutrient intake. By the time the smaller EM hens had reached peak production, much of their body reserves would have been diminished. Specific diet and lighting programs may be required to better match the requirements of each strain and reduce the differences observed in egg production. Strain specific management may become increasingly important in order to maximize production of saleable eggs in modern, early maturing, lower BW hens. Further research should also measure feed intake on a variety of diets and the timing of oviposition for individual hens throughout lay for various strains. This would help to identify both the extent to which strain specific management can increase sequence length and strain differences in factors contributing to flock rate of lay. The effect of multi-generation selection for increased prime sequence length on egg production and economic efficiency should also be examined.

IV.3 RESPONSE TO LIGHT INTENSITY

The results of the second experiment demonstrate that a modern strain of SCWL responds to photostimulation and reaches sexual maturity at an earlier age than a random-bred "antique" control strain. Modern commercial strains of SCWL are the product of strict genetic selection and breeding programs that have been successful at developing reproductively efficient birds. Age at first oviposition, reproductive morphology and the pullet's response to light appear to have been altered. Light intensity at photostimulation does not affect age of

first oviposition. However, the dose-like increase in ovary weight, oviduct weight and quantity of large yellow follicles (LYF) with light intensity demonstrates that light intensity affects reproductive development. Specifically, internal ovulation [evidenced by irreconcilable post ovulatory follicles (POF)] was almost completely eliminated by affecting oviduct growth through increasing light intensity. Genetic selection for reproductive efficiency in modern strains also appears to have greatly reduced internal ovulation in SCWL at sexual maturity.

The modern SCWL appears to have the ability to be stimulated by lower levels of light than its predecessors. Similar to the observations of Tucker and Charles (1993), it may be said that a modern strain of SCWL is more tolerant of low light intensities than previous stocks. However, if modern SCWL are able to respond to lower light levels, it becomes critical to rear pullets under management of strict light control to prevent early sexual development. Robinson *et al.* (1996) has previously described the effect of early photostimulation on modern strain SCWL pullets. Momentary or minute light leaks into a light-tight housing environment must be eliminated in order to prevent the ultra-sensitive modern strains from initiating sexual development at too early an age. The knowledge that strain differences exist provides reason to examine whether differences exist between various modern strains of SCWL in their response to photostimulation at different ages. With the development of highly specific genetic strains, it will be increasingly important to match the environmental and nutritional management practices to the particular strain of hen.

Yu et al. (1992) demonstrated the erratic oviposition and defective egg syndrome (EODES) is related to an excess number of LYF in broiler breeder hens. In the present study, the increased light intensity at photostimulation increased the quantity of LYF at sexual maturity. These data suggest that high light intensity of photostimulation may promote allocation of increasing proportions of energy toward follicular development and produce similar problems in egg-type hens as found in over-weight broiler breeders. Further research on the effects of light intensity on ovary morphology, subsequent egg production and timing of oviposition should be conducted to determine if this relationship truly exists.

IV.4 REFERENCES CITED

Anonymous, 1991. Shaver White Commercial Management Guide (T-05-I), Shaver Poultry Breeding Farms Limited, Cambridge, Ontario, Canada N1R 5V9.

Anonymous, 1992. Shaver Starcross 288 Commercial Management Guide, Shaver Poultry Breeding Farms Limited, Cambridge, Ontario, Canada N1R 5V9.

Etches, R.J., 1996. Reproduction in Poultry. CAB International. Wallingford, UK.

Hunton, P., 1990. Industrial breeding and selection. pp 985-1028. *in*: Poultry Breeding and Genetics. Developments in Animal and Veterinary Sciences, 22. Crawford, R.D., ed. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.

Robinson, F.E., T.A. Wautier, R.T. Hardin, J.L. Wilson, M. Newcombe, and R.I. McKay, 1996. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 2. Egg-type hens. Can. J. Anim. Sci. 76: 283-288.

Tucker, S.A., and D.R. Charles, 1993. Light intensity, intermittent lighting and feeding regimen during rearing as affecting egg production and egg quality. Br. Poult. Sci. 34: 255-266.

Yu, M.W., F.E. Robinson, R.G. Charles, and R. Weingardt, 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. Poultry Sci. 71: 1750-1761.

V. APPENDICES

APPENDIX A:

A.1.1 Data Sorted on Egg Production Variables into Upper / Lower Groups

A.1.1a Total Egg Numbers

When the data was sorted on the basis of total egg numbers, no difference was seen in 18 wk BW or carcass parameters at 68 wk between the upper and lower 50% or upper and lower 25% of the flock (Table A-1). The hens with the highest egg production also displayed no difference in ovary weight or the numbers of LYF and SYF at 68 wk than the hens with the lowest total egg production. There was a difference in total egg numbers between the groups, as expected when sorting by total egg numbers (Table A-2). Egg weight at 68 wk of age was highest in the lower 50% and 25% of hens sorted by total egg production. The 25% of the flock producing the highest number of eggs also had the highest production of normal eggs, although there were no differences in the production of soft-shelled, shell-less, double-yolked or abnormally shelled eggs between sorting groups by total egg numbers (Table A-2).

There was no difference in age at first oviposition in birds sorted by total egg numbers (Table A-2). This demonstrates that the highest total egg production was not a function of earlier sexual maturity in these birds. However, rate of lay was the primary cause of increased egg production, as there were differences in prime sequence length, number of sequences, average sequence length, average inter-sequence pause length and hen-day production parameters between the upper and lower 25 and 50% of the flock. Hen-day rate of egg production was higher in the upper 25 and 50% of hens sorted by total egg numbers for all 4 wk periods from 21 to 68 wk of age than in the lower 25 and 50% of the flock.

A.1.1b Prime Sequence Length

When the data was sorted on the basis of prime sequence length, there was no difference noticed in carcass traits at 68 wk between the upper and lower 50% or upper and

lower 25% of the flock (Table A-3). However, the hens which ranked in the upper 25% for prime sequence length had significantly lighter BW at 18 wk of age than the 25% of hens producing the shortest prime sequences. Total egg production was higher in both the 25 and 50% of hens laying longer prime sequences, and no statistical differences were seen in individual types of defective egg production (Table A-4). The 25% of hens laying longest prime sequences produced more normal eggs, although this difference was not statistically significant when sorted by upper and lower 50%. The average weight of the first egg and at 68 wk of age showed no difference between groups sorted for prime sequence length.

There was no difference in age at first oviposition in birds sorted by prime sequence length. However, hens which produced the longest prime sequences (upper 25 and 50%) also produced the most total eggs with the longest average sequences. Average inter-sequence pause length was not affected by sorting on the basis of prime sequence length (Table A-4). Average hen-day production from photostimulation and from first oviposition was higher in the hens laying the longest prime sequences. Hen-day rate of egg production was highest in the upper 25 and 50% of hens sorted by prime sequence length for the 4 wk periods from 25 to 60 wk of age.

A.1.1c Age at First Oviposition

When the data were sorted on the basis of age at first oviposition, a difference was seen in BW at 18 and 66 wk of age (Table A-5). The hens which reached sexual maturity at the earliest age were heavier at 18 wk of age, but were lighter at the end of lay. The weights of breast muscle, abdominal fat pad, liver and ovary at 68 wk of age were also lower in the 25% of hens which had reached sexual maturity at the youngest age when compared to the 25% of the oldest hens reaching sexual maturity. This trend was also seen in the upper and lower 50% of the flock, although only the differences in breast muscle and liver weight were significant. Table A-6 illustrates that earlier sexual maturity reduced initial egg weight. There was no difference in normal eggs produced between any of the groups sorted by age at first

oviposition. This results from the significant increases in defective eggs produced by the hens which reached sexual maturity at an earlier age, as seen by soft-shelled eggs when comparing the earlier and later maturing 50% of the flock, and in double-yolked and abnormally-shelled eggs when comparing the early and later maturing 25% of the flock.

Table A-6 illustrates that sorting on the basis of earlier sexual maturity demonstrates increased average hen-day production from photostimulation, specifically from increased rates of production in the initial laying wks (17 to 24 wk), There is no difference in rate of egg production throughout the remainder of lay to 68 wk of age between early and late-maturing birds. In the 25 and 50% of hens with the lowest age at sexual maturity, total egg production numbers were not increased by the full potential which would be allowed by their reduced age at sexual maturity. The length of laying sequences was not affected by age at first oviposition.

Table A-1. Mean values of carcass traits from 101 Single Comb White Leghorn hens housed to 68 wk of age, sorted on the basis of total egg numbers produced, flock mean (n=101), the upper 50% (n=50), the lower 50% (n=51), the upper 25% (n=25), and the lower 25% (n=25) of the flock

Variable	Flock mean	Upper 50% of Flock	Lower 50% of Flock	SEM	Upper 25% of Flock	Lower 25% of Flock	SEM
18 wk BW (g)	1284.2	1277.9	1290.3	10.7	1274.0	1287.5	14.6
66 wk BW (g)	1894.1	1867.4	1920.3	35.6	1926.3	1934.6	52.5
Breast muscle weight (g)	212.5	212.7	212.3	5.6	218.9	220.8	8.4
Liver weight (g)	36.4	35.0	37.8	1.5	36.7	40.8	2.5
Fat pad weight (g)	98.8	94.4	103.1	5.4	96.7	103.8	7.8
Ovary weight (g)	53.1	53.7	52.5	1.2	54.1	52.4	1.7
Quantity of LYF[1]	5.3	5.4	5.2	0.1	5.5	5.1	0.1
Quantity of SYF[2]	13.0	12.7	13.4	0.7	12.8	13.3	1.1

[a,b] Means compared between either the upper and lower 50% or between the upper and lower 25% with different superscripts are significantly different (P < 0.05). SEM listed for lowest n.

[1] LYF = large yellow follicles

[2] SYF = small yellow follicls

Table A-2. Mean values of egg shell quality and production traits for 101 Single Comb White Leghorn hens housed to 68 wk of age, sorted on the basis of total egg numbers produced, flock mean (n=101), the upper 50% (n=50), the lower 50% (n=51), the upper 25% (n=25), and the lower 25% (n=25) of the flock

Variable	Flock mean	Upper 50% of flock	Lower 50% of flock	SEM	Upper 25% of flock	Lower 25% of flock	SEM
1st egg (g)	40.0	39.1	40.9	0.8	38.7	40.7	1.4
68 wk egg weight (g)	62.9	61.2[b]	64.5[a]	0.6	59.6[b]	64.8[a]	0.9
Total eggs[1]	297.4	311.9[a]	283.2[b]	1.5	319.4[a]	273.4[b]	1.6
Normal eggs	289.5	304.4	274.9	2.5	312.0[a]	263.4[b]	3.6
Soft shelled eggs	2.5	2.1	2.9	0.9	1.9	4.4	1.6
Shell-less eggs	1.6	1.5	1.7	0.4	1.2	1.7	0.4
Double-yolked eggs	1.9	2.1	1.8	0.3	1.8	1.5	0.4
Abnormal shelled eggs	1.9	1.9	2.0	0.7	2.4	2.5	1.3
Age at 1st Oviposition (d)	138.8	137.9	139.7	0.9	137.3	140.5	1.3
Prime Sequence length (d)	61.5	77.6[a]	45.7[b]	4.9	97.6[a]	39.9[b]	7.3
Number of Sequences	35.7	26.0[b]	45.1[a]	1.7	19.8[b]	50.6[a]	2.5
Mean sequence length (d)	10.7	14.9[a]	6.6[b]	0.8	19.4[a]	5.8[b]	1.3
Mean pause length (d)	1.16	1.10[b]	1.22[a]	0.03	1.08[b]	1.29[a]	0.05
Hen-day production 1[2] %	85.0	89.1[a]	80.9[b]	0.4	91.3[a]	78.1[b]	0.5
Hen-day production 2[3] %	88.2	92.3[a]	84.2[b]	0.5	94.3[a]	81.5[b]	0.5

[a,b] Means compared between either the upper and lower 50% or between the upper and lower 25% with different superscripts are significantly different ($P < 0.05$). SEM listed for lowest n.

[1] Data sorted on the basis of total egg production.

[2] Hen-day production 1 calculated by total eggs divided by hen-days from photostimulation to 68 wk.

[3] Hen-day production 2 calculated by total eggs divided by hen-days from first oviposition to 68 wk.

Table A-3. Mean values of carcass traits from 101 Single Comb White Leghorn hens housed to 68 wk of age, sorted on the basis of prime sequence length (d), flock mean (n=101), the upper 50% (n=50), the lower 50% (n=51), the upper 25% (n=25), and the lower 25% (n=25) of the flock

Variable	Flock mean	Upper 50% of Flock	Lower 50% of Flock	SEM	Upper 25% of Flock	Lower 25% of Flock	SEM
18 wk BW (g)	1284.2	1272.3	1295.8	10.6	1262.4[b]	1323.4[a]	15.5
66 wk BW (g)	1894.1	1900.3	1888.1	35.8	1949.7	1988.5	49.7
Breast muscle weight (g)	212.5	215.1	209.9	5.6	224.1	221.7	7.4
Liver weight (g)	36.4	35.4	37.4	1.5	36.8	40.2	2.6
Fat pad weight (g)	98.8	101.1	96.4	5.4	102.1	112.2	7.4
Ovary weight (g)	53.1	53.7	52.5	1.2	56.5	52.9	1.6
Quantity of LYF[1]	5.3	5.4	5.2	0.1	5.4	5.1	0.1
Quantity of SYF[2]	13.0	13.4	12.7	0.7	13.1	12.2	1.0

[a,b] Means compared between either the upper and lower 50% or between the upper and lower 25% with different superscripts are significantly different ($P < 0.05$). SEM listed for lowest n.
[1] LYF = large yellow follicles
[2] SYF = small yellow follicls

Table A-4. Mean values of egg shell quality and production traits for 101 Single Comb White Leghorn hens housed to 68 wk of age, sorted on the basis of prime sequence length (d), flock mean (n=101), the upper 50% (n=50), the lower 50% (n=51), the upper 25% (n=25), and the lower 25% (n=25) of the flock

Variable	Flock mean	Upper 50% of flock	Lower 50% of flock	SEM	Upper 25% of flock	Lower 25% of flock	SEM
1st egg weight (g)	40.0	39.6	40.4	0.8	40.3	39.4	1.2
68 wk egg weight (g)	62.9	62.6	63.1	0.7	62.2	63.9	1.0
Total eggs	297.4	306.0[a]	289.0[b]	2.2	307.8[a]	285.0[b]	3.2
Normal eggs	289.5	300.4	278.7	2.9	302.9[a]	273.2[b]	4.0
Soft-shelled eggs	2.5	1.3	3.7	0.9	1.4	4.4	1.3
Shell-less eggs	1.6	1.3	1.9	0.4	1.1	2.1	0.7
Double-yolked eggs	1.9	1.8	2.1	0.3	1.2	1.8	0.4
Abnormal shelled eggs	1.9	1.2	2.6	0.6	1.1	3.4	1.1
Age at 1st Oviposition (d)	138.8	138.9	138.7	0.9	140.6	139.0	1.3
Prime sequence length(d)[1]	61.5	90.6[a]	33.0[b]	3.5	115.8[a]	23.4[b]	4.0
Number of Sequences	35.7	26.7[b]	44.4[a]	1.8	22.8[b]	51.2[a]	2.5
Mean sequence length (d)	10.7	14.3[a]	7.1[b]	0.9	17.2[a]	5.8[b]	1.3
Mean pause length (d)	1.16	1.18	1.15	0.03	1.16	1.12	0.03
Hen-day production 1[2] %	85.0	87.4[a]	82.6[b]	0.6	87.9[a]	81.4[b]	0.9
Hen-day production 2[3] %	88.2	90.8[a]	85.7[b]	0.6	91.8[a]	84.5[b]	0.9

[a,b] Means compared between either the upper and lower 50% or between the upper and lower 25% with different superscripts are significantly different ($P < 0.05$). SEM listed for lowest n.

[1] Data sorted on the basis of prime sequence length (d)

[2] Hen-day production 1 calculated by total eggs divided by hen-days from photostimulation to 68 wk.

[3] Hen-day production 2 calculated by total eggs divided by hen-days from first oviposition to 68 wk.

Table A-5. Mean values of carcass traits from 101 Single Comb White Leghorn hens housed to 68 wk of age, sorted on the basis of age at first oviposition (d), flock mean (n=101), the upper 50% (n=50), the lower 50% (n=51), the upper 25% (n=25), and the lower 25% (n=25) of the flock

Variable	Flock mean	Upper 50% of Flock	Lower 50% of Flock	SEM	Upper 25% of Flock	Lower 25% of Flock	SEM
18 wk BW (g)	1284.2	1318.1[a]	1249.5[b]	9.5	1350.4[a]	1240.6[b]	14.0
66 wk BW (g)	1894.1	1832.7[b]	1956.8[a]	34.7	1747.2[b]	1953.3[a]	49.7
Breast muscle weight (g)	212.5	201.8[b]	223.4[a]	5.4	185.6[b]	229.3[a]	7.2
Liver weight (g)	36.4	33.7[b]	39.2[a]	1.5	31.7[b]	39.4[a]	2.1
Fat pad weight (g)	98.8	94.6	103.0	5.4	82.8[b]	102.4[a]	6.8
Ovary weight (g)	53.1	51.6	54.6	1.2	49.9[b]	55.0[a]	1.8
Quantity of LYF[1]	5.3	5.2	5.3	0.1	5.3	5.1	0.1
Quantity of SYF[2]	13.0	12.7	13.3	0.7	12.0	13.0	0.9

[a,b] Means compared between either the upper and lower 50% or between the upper and lower 25% with different superscripts are significantly different ($P < 0.05$). SEM listed for lowest n.
[1] LYF = large yellow follicles
[2] SYF = small yellow follicls

Table A-6. Mean values of egg shell quality and production traits for 101 Single Comb White Leghorn hens housed to 68 wk of age, sorted on the basis of age at first oviposition (d), flock mean (n=101), the upper 50% (n=50), the lower 50% (n=51), the upper 25% (n=25), and the lower 25% (n=25) of the flock

Variable	Flock mean	Upper 50% of flock	Lower 50% of flock	SEM	Upper 25% of flock	Lower 25% of flock	SEM
1st egg weight (g)	40.0	38.4[b]	41.6[a]	0.8	38.6[b]	43.0[a]	1.4
68 wk egg weight (g)	62.9	62.0	63.7	0.7	61.5[b]	64.8[a]	0.8
Total eggs	297.4	301.0[a]	293.8[b]	2.5	304.6[a]	290.8[b]	3.2
Normal eggs	289.5	290.2	288.7	3.3	290.5	286.2	4.4
Soft-shelled eggs	2.5	3.8[a]	1.2[b]	0.9	4.2	1.6	1.2
Shell-less eggs	1.6	2.1	1.1	0.4	2.4	1.7	0.5
Double-yolked eggs	1.9	2.7[a]	1.2[b]	0.3	3.4[a]	0.6[b]	0.3
Abnormal shelled eggs	1.9	2.3	1.5	0.7	4.0[a]	0.9[b]	1.1
Age at 1st egg (d)[1]	138.8	134.0[b]	143.7[a]	0.6	130.4[b]	146.2[a]	0.7
Prime Sequence length (d)	61.5	57.5	65.6	5.3	56.0	61.8	7.3
Number Sequences	35.7	37.4	33.8	2.2	38.6	35.6	3.1
Mean sequence length (d)	10.7	10.0	11.5	1.0	9.7	10.3	1.3
Mean pause length (d)	1.16	1.2	1.1	0.03	1.2	1.1	0.03
Hen-day production 1[2] %	85.0	86.0[a]	83.9[b]	0.7	87.0[a]	83.1[b]	0.9
Hen-day production 2[3] %	88.2	88.0	88.4	0.7	88.1	88.2	1.0

[a,b] Means compared between either the upper and lower 50% or between the upper and lower 25% with different superscripts are significantly different ($P < 0.05$). SEM listed for lowest n.

[1] Data sorted on the basis of age at first oviposition (d)

[2] Hen-day production 1 calculated by total eggs divided by hen-days from photostimulation to 68 wk.

[3] Hen-day production 2 calculated by total eggs divided by hen-days from first oviposition to 68 wk.

APPENDIX B:

Regression Equations for A-group Data from 17 to 23 wk for experiment II: Ovarian morphology, egg production and laying profiles in two commercial strains of egg-type hens differing in age at sexual maturity. (x = age in weeks). EM=Early maturing Babcock B300; LM= Later maturing Shaver White.

BW
EM $y = -16669.0000 + 2440.9345x - 111.1214x^2 + 1.7083x^3$
LM $y = 24090.0000 - 3753.1460x + 200.4095 x^2 - 3.4778x^3$

BREAST MUSCLE WT
EM $y = -6107.1814 + 894.6956x - 42.1646x^2 + 0.6583x^3$
LM $y = -1001.8286 + 123.44476x - 3.5388x^2 + 0.0183x^3$

FATPAD WT
EM $y = -3300.8876 + 484.7929x - 23.6529x^2 + 0.3878x^3$
LM $y = 3541.9976 - 565.4441x + 29.6727 x^2 - 0.5086x^3$

LIVER (WET) WT
EM $y = -1195.0176 + 165.3219x - 7.3582x^2 + 0.1078^3$
LM $y = 617.2543 - 107.9682x + 6.2908x^2 - 0.1183x^3$

OVIDUCT WT
EM $y = 2770.6343 - 457.7331x + 24.7005x^2 - 0.4317x^3$
LM $y = 4112.8429 - 637.2787x + 32.4379 x^2 - 0.5392x^3$

OVARY WT
EM $y = 4209.9957 - 658.2232x + 33.7582x^2 - 0.5650x^3$
LM $y = 2639.1043 - 388.2533x + 18.5973x^2 - 0.2875x^3$

STROMA WT
EM $y = 220.5571 - 34.6620x + 1.7740x^2 - 0.0292x^3$
LM $y = -191.8500 + 31.1136x - 1.6887 x^2 + 0.0308x^3$

NUMBER OF SYF
EM $y = 256.2429 - 40.6750x + 2.0726x^2 - 0.0333x^3$
LM $y = -474.8667 + 75.7552x - 4.0417x^2 + 0.0722x^3$

NUMBER OF LYF
EM $y = 590.8524 - 96.2385x + 5.1274x^2 - 0.0889x^3$
LM $y = 782.7238 - 118.9290x + 5.9405 x^2 - 0.0972x^3$

PLASMA LIPID CONCENTRATION
EM $y = -149.3082 + 16.4032x - 0.5086x^2 + 0.0036x^3$
LM $y = 804.4434 - 124.8606x + 6.4052x^2 - 0.1083x^3$

DRY LIVER WT
EM $y = -512.3316 + 67.4942x - 2.7701x^2 + 0.0362x^3$
LM $y = 423.5359 - 72.9578x + 4.2059 x^2 - 0.0786x^3$

LIVER LIPID CONCENTRATION %

EM $y = -4151.3003 + 594.9159x - 28.0156x^2 + 0.4363x^3$

LM $y = 3733.2280 - 606.5904x + 32.5752x^2 - 0.5753x^3$

LIVER LIPID WT

EM $y = -568.3494 + 74.5284x - 3.1341x^2 + 0.0423x^3$

LM $y = 791.1640 - 130.5670x + 7.1033x^2 - 0.1269x^3$

TOTAL LYF WT

EM $y = 3989.4386 - 623.5612x + 31.9842x^2 - 0.5358x^3$

LM $y = 2830.9543 - 419.3669x + 20.2860x^2 - 0.3183x^3$

BREAST MUSCLE WT AS A % OF BW

EM $y = -292.3314 + 45.1835x - 2.1924x^2 + 0.0349x^3$

LM $y = -324.0234 + 50.3765x - 2.4652x^2 + 0.0396x^3$

FATPAD WT AS A % OF BW

EM $y = -249.2920 + 36.7182x - 1.7925x^2 + 0.0293x^3$

LM $y = 173.5256 - 28.3252x + 1.5160x^2 - 0.0264x^2$

LIVER WT AS A % OF BW

EM $y = -87.3863 + 12.5195x - 0.5770x^2 + 0.0087x^3$

LM $y = 8.7105 - 1.9409x + 0.1437x^2 - 0.0032x^3$

OVIDUCT WT AS A % OF BW

EM $y = 211.5935 - 34.9118x + 1.8859x^2 - 0.0331x^3$

LM $y = 242.8249 - 37.8114x + 1.9334x^2 - 0.0322x^3$

OVARY WT AS A % OF BW

EM $y = 332.9934 - 52.1868x + 2.6865x^2 - 0.0452x^3$

LM $y = 171.1335 - 25.1718x + 1.2048x^2 - 0.0186x^3$

STROMA WT AS A % OF BW

EM $y = 20.8930 - 3.2748x + 0.1682x^2 - 0.0028x^3$

LM $y = -14.8018 + 2.3883x - 0.1287x^2 + 0.0023x^3$

TOTAL LYF AS A % OF BW

EM $y = 312.1004 - 48.9121x + 2.5183x^2 - 0.0424x^3$

LM $y = 185.9353 - 27.5601x + 1.3335x^2 - 0.0209x^3$

PLASMA ESTRADIOL CONCENTRATION

EM $y = 80966 - 13427x + 740.5474x^2 - 13.5636x^3$

LM $y = 87623 - 14338x + 779.7331x^2 - 14.0727x^3$

HEN DAY EGG PRODUCTION CURVE FROM 18 to 68 WK OF AGE (C-group)

EM $y = -21.323605 + 2.720992x - 0.128219x^2 + 2.924*10^{-3}x^3 - 3.2410*10^{-5}x^4 + 1.400*10^{-7}x^5$

LM $y = -21.597028 + 2.691558x - 0.124392x^2 + 2.793*10^{-3}x^3 - 3.0556*10^{-5}x^4 + 1.305*10^{-7}x^5$

APPENDIX C:

Additional data for follicle weights and egg production parameters for experiment II, Ovarian morphology, egg production and laying profiles in two commercial strains of egg-type hens differing in age at sexual maturity. (not necessarily referred to in text)

Table C-1. Large yellow follicle (LYF) weight (g) at sexual maturity in two strains of Single Comb White Leghorn hen differing in age at sexual maturity. Means within a row with no common superscripts differ significantly ($P < 0.05$). SEM listed for lowest n. EM=Early Maturing; LM=Later Maturing.

Trait	n	EM	n	LM	SEM
F1	8	8.2	3	8.4	0.5
F2	20	8.1	20	8.4	0.2
F3	19	6.7	20	7.0	0.3
F4	19	5.5	19	5.5	0.3
F5	18	3.8	16	4.1	0.4
F6	15	3.2	13	2.9	0.4
F7	11	2.6	12	1.9	0.3
F8	8	20	6	1.3	0.4
F9	6	1.4	2	1.3	0.4
F10	3	0.9	0	–	0.1
F11	1	0.8	0	–	–

Table C-2. Large yellow follicle (LYF) weight (g) at 68 wk of age in two strains of Single Comb White Leghorn differing in age at sexual maturity. Means within a row with no common superscripts differ significantly ($P < 0.05$). SEM listed for lowest n. EM=Early Maturing; LM=Later Maturing

Trait	n	EM	n	LM	SEM
F1	50	17.4	52	17.2	0.3
F2	50	13.5	52	13.2	0.3
F3	50	9.1	52	9.1	0.3
F4	50	5.0	52	5.2	0.3
F5	46	2.2	47	2.3	0.2
F6	15	1.2	18	1.4	0.2

Table C-3. Data used to construct sequence length profiles from 18 to 68 wk for two strains of Single Comb White Leghorn hens differing in age at sexual maturity. See Figure II-3. Strain profiles differed when tested by Kolmogorov-Smirnov test ($P < 0.05$). EM=Early Maturing (n=50); LM=Later Maturing (n=51).

Week	EM	LM	Week	EM	LM	Week	EM	LM	Week	EM	LM
18	1.4	–	31	37.8	64.2	44	16.2	37.7	57	8.8	14.0
19	11.2	1.7	32	39.8	63.4	45	14.8	35.2	58	9.1	13.7
20	19.4	17.1	33	41.3	63.3	46	13.4	33.1	59	8.5	12.7
21	26.5	32.0	34	41.6	63.2	47	12.8	30.9	60	7.7	11.9
22	32.9	43.9	35	39.5	63.0	48	12.6	27.6	61	7.8	10.8
23	38.0	50.9	36	38.9	59.5	49	11.8	21.4	62	7.9	9.5
24	41.5	52.0	37	36.2	60.6	50	11.4	20.6	63	7.7	9.7
25	43.8	52.1	38	32.9	58.0	51	11.1	19.4	64	7.6	9.6
26	45.6	54.9	39	27.2	55.8	52	11.6	16.8	65	7.0	9.5
27	43.0	58.3	40	22.4	53.4	53	9.8	18.0	66	6.7	9.0
28	42.1	59.8	41	19.2	48.8	54	8.1	15.9	67	6.6	8.2
29	39.9	60.7	42	18.7	44.7	55	8.4	15.9	68	5.6	7.3
30	37.3	63.0	43	18.4	39.4	56	8.0	15.2	–	–	–

Table C-4. Data used to construct pause length profiles from 18 to 68 wk for two strains of Single Comb White Leghorn hens differing in age of sexual maturity. Strain profiles did not differ when tested by Kolmogorov-Smirnov test ($P > 0.05$). EM=Early Maturing (n=50); LM=Later Maturing (n=51)

Week	EM	LM	Week	EM	LM	Week	EM	LM	Week	EM	LM
18	1.5	–	31	1.0	1.1	44	1.3	1.1	57	2.5	1.2
19	1.5	–	32	1.0	1.2	45	1.1	1.3	58	2.6	1.1
20	2.0	1.8	33	2.9	1.3	46	1.2	1.4	59	1.5	1.3
21	3.7	2.2	34	1.1	1.0	47	1.3	1.1	60	1.3	1.3
22	4.7	4.0	35	1.0	1.0	48	1.2	1.1	61	1.3	2.7
23	4.1	4.6	36	1.0	1.1	49	1.2	1.2	62	1.8	5.2
24	1.2	2.0	37	1.1	1.4	50	1.1	1.1	63	1.8	4.6
25	2.0	1.5	38	1.3	1.2	51	1.1	1.2	64	1.4	5.6
26	1.1	1.6	39	1.2	1.4	52	1.3	1.1	65	2.1	5.3
27	1.0	1.5	40	1.1	1.3	53	1.3	1.2	66	3.4	4.3
28	1.5	1.0	41	1.2	1.1	54	1.3	1.1	67	3.5	1.2
29	1.0	1.2	42	1.6	1.1	55	1.2	1.2	68	3.6	1.3
30	1.1	1.3	43	1.5	1.1	56	1.4	1.2	–	–	–