THE EFFECT OF PHOTOPERIOD AND FEEDING TIME ON BROILER BREEDER EGGSHELL QUALITY AND OVIPOSITION TIME

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DECLARATION

We hereby declare that the research reported in this thesis does not contain material which has been accepted for the award of any other degree or diploma in another University and, to the best of our knowledge, does not contain material previously published or written by another person, except where due reference is made in the text.

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GLOSSARY OF AVIAN PHOTOPERIODIC TERMINOLOGY, UNIT ABBREVIATIONS AND METHODS OF EXPRESSING LIGHTING REGIMENS

To help the lay reader of this thesis, a glossary of photoperiodic terminology, a list of unit abbreviations, and a description of the methods used to express lighting regimens have been included. Unless otherwise referenced in the text, the definitions in the glossary and the description of the methods used in expressing lighting regimens were published previously by Lewis and Perry (1990).

GLOSSARY

Ahemeral. Applied to cycles which are either longer or shorter than 24 h.

Candela. A unit of luminous intensity: the luminous flux emitted by a point source per unit solid angle, which has a radiant intensity in that direction of 1.464×10^{-3} watts per steradian.

Circadian. An endogenous rhythm whose free running period is close to, but not usually equal to, 24 h.

Constant conditions. Conditions when an environmental element remains unchanged, and under which an endogenous rhythm expresses its natural frequency, e.g. continuous darkness.

Cycle. A sequence of events which is exactly repeated.

Dawn. The dark-light interface which the animal appears to interpret as the beginning of the day or subjective day.

Day. The period between the dark-light interface which the animal interprets as dawn and the light-dark interface which the animal interprets as dusk.

Daylength. The time which elapses between the dark-light interface which the animal interprets as dawn and the light-dark interface which the animal interprets as dusk.

Diurnal. Applied to events which occur during the day or subjective day.

Dusk. The light-dark interface which the animal appears to interpret as the end of the day or subjective day.

Entraining agent. An external signal which causes entrainment of an endogenous rhythm, and which is itself periodic, e.g. a temperature cycle. Synonymous with *Zeitgeber*.

Entrainment. Adjustment of an internal rhythm so that it synchronises with an external cycle, e.g. light and darkness.

Foot-candle. A former unit of luminous intensity. The illumination of a surface area of 1 ft^2 receiving a luminous flux of 1 lumen (equivalent to 0.093 lux).

Free-running rhythm. An endogenous rhythm which continues under constant conditions.

Frequency. The number of complete cycles of a periodic process occurring per unit of time.

Hemeral. Applied to cycles of 24 h duration.

Interrupted lighting regimen. A series of alternating photoperiods and scotoperiods, which may or may not be interpreted by the animal as a day and night; synonymous with intermittent lighting.

Lumen. A unit of luminous flux. The rate of flow of light energy from a light source which is emitted in a solid angle of 1 steradian with a luminous intensity of 1 candela.

Luminous flux. The flow of energy from a light source, measured in lumens.

Luminous intensity. The degree of illumination of a surface, measured in lux.

Lux. A unit of luminous intensity. The illumination of a surface area of 1 m^2 receiving a luminous flux of 1 lumen, (equivalent to 10.764 foot-candles).

Night. The period between the light-dark interface which the animal interprets as dusk and the dark-light interface which the animal interprets as dawn.

Nocturnal. Applied to events which occur during the night.

Open period. The period during which the preovulatory release of luteinising hormone (LH) occurs (Wilson and Cunningham, 1984).

Oviposition. The act of laying an egg (Blood and Studdert, 1988).

Ovulation. The release of an ovum from the ovary (Stephens, 1996).

Period. The time which elapses before an event or rhythm recurs.

Phase angle. The time that elapses between an entraining agent and a phase point on a biological rhythm, e.g. between dusk and minimum deep body temperature.

Phase point. A nominated point in a biological rhythm, e.g. maximum deep body temperature.

Phase relationship. The relationship between two entraining agents, or between an entraining agent and a rhythm under its control.

Phase response curve. A curve which describes the extent of the phase shift of a rhythm (advance or delay, in hours) that occurs if a light pulse is given at a particular circadian time.

Phase shift. A change in the phase relationship between two entraining agents, or between an entraining agent and a rhythm under its control.

Photoperiod. A period of natural or artificial illumination.

Scotoperiod. A period of darkness (or low luminous intensity which is interpreted by the animal as darkness).

Skeleton photoperiod. A photoperiod interrupted by one or more periods of darkness, but interpreted by the hen as a single photoperiod.

Subjective day. A series of light and dark periods which the animal appears to interpret as a single day. It may also be that period during conditions of constant darkness or dim light which the animal appears to interpret as a single day.

Zeitgeber. An external signal which causes entrainment of an endogenous rhythm, and which is itself periodic, e.g. a temperature cycle. Synonymous with *Entraining agent.*

UNIT ABBREVIATIONS

D	darkness
h	hour
L	light
min	minute
W	watt

METHODS OF EXPRESSING LIGHTING REGIMENS

Periods of light are represented by their duration in hours followed by an 'L', e.g. 16 h light is described as 16L.

Periods of darkness are represented by their duration in hours followed by a 'D', e.g. 8 h darkness is described as 8D.

Thus, conventional lighting regimens are described as the duration of the light period (h) followed by an 'L', with a colon separating it from the duration of darkness (h) followed by a 'D', e.g. 16 h light followed by 8 h darkness would be described as 16L:8D.

Interrupted lighting regimens are described as the duration of each period of light (h) followed by an 'L' with a colon separating them from the duration of each succeeding period of darkness (h) followed by a 'D', e.g. 2 h light, 4 h darkness, 8 h light and 10 h darkness would be described as 2L:4D:8L:10D.

ABSTRACT

This study was conducted to determine the effect of photoperiod and feeding time on oviposition time and eggshell quality of broiler breeders. Five experiments were conducted in total.

The effect of photoperiod on oviposition time was tested in Experiments 1 and 2. Experiment 1 involved 3200 33-week old broiler breeder hens housed in floor pens and subjected to photoperiods of 10, 11, 12, 13, 14 or 16 h. Experiment 2 used 120 37-week old broiler breeders, housed in individual cages in each of two light-proof rooms; one room on 8-h and the other on 16-h photoperiods. Birds in Experiment 1 were also used to determine the effect of photoperiod on eggshell quality, although they were 52 weeks of age when shell quality was assessed.

The effect of feeding time on the aforementioned parameters was tested in three experiments. Experiment 3 involved 432 24-week old broiler breeders housed in individual cages and subjected to a 14-h photoperiod from 07.00 to 21.00. The birds were fed at 07.30, 09.30, 11.30, 13.30 or 15.30. In one further treatment, birds were fed half the daily feed allocation at 07.30 and half at 15.30. Experiment 4 made use of 800 57-week old broiler breeder females housed on litter floor pens and subjected to a 14-h photoperiod from 05.00 to 19.00. The birds were fed at 07.30, 10.00, 13.00 or 15.30. In Experiment 5, 240 35-week old broiler breeder females were subjected to a 16-h photoperiod from 07.00 to 23.00. The feeding times tested in Experiment 5 were 07.30, 10.00, 13.00 and 15.30.

Mean oviposition time was delayed relative to dawn by approximately 0.5 h for each 1-h increase in photoperiod up to 14 h, but was similar for 14 and 16-h photoperiods. The time when half a day's eggs were laid was also delayed relative to dawn by approximately 0.5 h for each 1-h increase in photoperiod, although this trend continued through to 16 h. The rate of change in mean oviposition time for each 1-h increase in ≤14-h photoperiod was similar to that reported for early and modern egg-type hybrids,

but, compared with modern genotypes, time of lay itself was 1 h later than white-egg and 2.5 h later than brown-egg hybrids. At photoperiods ≤12.25 h, the number of eggs laid before dawn increased by 4.5% for each 1-h reduction in daylength.

Egg weight increased by 0.31 g, shell weight decreased by 30 mg, and shell thickness index decreased by 0.57 mg/cm^2 for each 1-h increase in photoperiod. Changes in egg weight and eggshell thickness index might be overstated because eggs were collected at the same chronological time. In spite of this, the effect of time of egg-laying within the day was minimal in comparison, and did not negate the conclusion that egg weight increases, and shell weight and thickness index decrease with lengthening photoperiods. The effect of photoperiod on eggshell quality was not due to differences in the rate of lay between treatments. Shell weight was unaffected by time of lay.

Mean eggshell thickness was increased significantly by 3.5 μm (approximately 1 %) per hour delay in feeding time when hens were housed in individual cages. However, eggshell thickness was not significantly affected by feeding time when birds were housed on litter floors. Mean oviposition time was delayed relative to lights-on by 5 min per hour delay in feeding time. Egg weight was not significantly affected by feeding time, suggesting that differences in shell thickness and oviposition times were not due to increased transit times through the oviduct.

Data presented in this thesis suggest that the current commercial practice of subjecting broiler breeder flocks to photoperiods that are in excess of the photoperiod required for maximum egg production is questionable. Apart from being unnecessary and costly, providing broiler breeders with excessively long photoperiods may be a cause of depressed eggshell thickness with consequential low hatchability. Eggshell quality can be improved by delaying the time of feeding, although improvements may only be marginal in broiler breeder flocks that are housed on litter floors. However, delaying the time of feeding may cause a delay in oviposition times. Producers who wish to implement delayed feeding should thus consider the management implications of eggs being laid later in the day.

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CHAPTER 1

GENERAL INTRODUCTION

A positive correlation exists between hatchability of eggs and shell thickness. In order to produce the maximum number of broiler chicks, it is thus essential that broiler breeder flocks be supplied with nutritional and environmental conditions that maintain high levels of shell quality whilst sustaining maximum egg production. Apart from the supply of calcium and vitamin D_3 to broiler breeder hens, two important, but less obvious, considerations in maintaining good shell quality are the time at which the birds are fed, and the number of hours of light to which the birds are subjected each day.

In order to improve eggshell thickness, broiler breeder producers have attempted feeding their flocks later in the day. Although previous studies have been conducted to determine the effect of time of feeding on eggshell quality, results are contradictory. Furthermore, a potential concern with delayed feeding is a delay in the time of oviposition, which may result in egg collection and grading problems. Therefore, there is a need for further research into the effect of feeding time on eggshell quality and oviposition time of broiler breeders.

Eggshell thickness of laying-type hybrids is negatively correlated with photoperiod. Such a relationship has not been studied in broiler breeders. Numerous commercial operations subject broiler breeder flocks to long photoperiods, which are in excess of the photoperiod required for maximum egg production. For example, in South Africa, it is common to find broiler breeder flocks with a lighting schedule of 18L:6D during the laying period. This practice may be a cause of depressed eggshell thickness with consequential low hatchability. Research into the effect of photoperiod on broiler breeder eggshell quality is thus necessary.

The influence of the length of the photoperiod on the time of oviposition has been extensively studied in laying-type hybrids. However, no such studies have been performed in broiler breeders. This lack of knowledge alone makes research in this field worthwhile. Furthermore, due to oviposition time being of importance in commercial broiler breeder operations with

regard to egg collection and grading, and, due to the relationship between shell formation and ovulation time, such research is of practical relevance.

The work herein is a study of the influence of photoperiod and feeding time on oviposition time and eggshell thickness of broiler breeders.

CHAPTER 2

LITERATURE REVIEW

2.1 PHOTOPERIOD AND OVIPOSITION TIME

2.1.1 The open period for LH release

In the domestic hen, ovulations occur in sequences that vary in length from two to as many as 360 eggs (Etches, 1996a). The ovulatory cycle is the interval between consecutive ovulations. Table 2.1 shows the times of successive ovipositions in sequences of varying lengths in laying hens. From this Table, it is evident that oviposition, and hence ovulation, under standard conditions of light and darkness, is restricted to about eight hours of the day. This eight-hour period when spontaneous ovulation occurs was conventionally referred to as the open period (Fraps, 1955). Since ovulation is brought about by increases in blood concentrations of luteinising hormone (LH) and gonadal steroids eight to four hours earlier, the open period is now generally referred to as the period during which the preovulatory release of LH occurs (Wilson and Cunningham, 1984).

Table 2.1 *Times of successive ovipositions of laying hens under a 14L:10D photoschedule (lights on from 06.00 to 20.00). The last ovulation of a sequence is followed by a day during which ovulation does not occur. (Etches, 1996a).*

Sequence	Position of ovipositions in sequence								
length	1	2	3	4	5	6	7	8	9
2	9.05	13.30	-	-	-	-	-	-	-
3	8.41	11.26	15.15	-	-	-	-	-	-
4	8.01	10.09	12.03	15.23	-	-	-	-	-
5	7.24	9.22	10.26	11.46	15.05	-	-	-	-
6	7.33	9.20	10.34	11.30	12.34	15.40	-	-	-
7	7.45	9.12	10.10	10.51	11.39	12.38	15.28	-	-
8	7.36	8.59	9.57	10.26	10.47	11.43	12.49	15.44	-
9	7.18	8.39	9.25	9.44	9.53	10.26	10.59	12.02	15.18

Since the anatomical location of the open period for LH release has not been located or described in endocrine terms, the physiological basis of the mechanisms which determine the precise timing of a sequence of ovulations and the restriction of follicular rupture to eight hours of the day are unknown. The absence of such knowledge restricts understanding of the open period to theories and conclusions derived from responses of populations of chickens to various light-dark cycles. These studies have shown that the open period for LH release possesses circadian characteristics.

The effect of the light-dark cycle on time of oviposition was investigated by Warren and Scott (1936). These researchers kept birds on a 12L:12D photoschedule and then subjected the birds to continuous light. After a few days of continuous illumination, ovipositions were distributed throughout day and night, suggesting that the light-dark cycle had an influence on oviposition time. A number of subsequent changes to the photoschedule demonstrated that the light-dark cycle did indeed regulate the time of oviposition. Numerous other shift experiments showed that ovipositions were restricted mainly to the period of illumination, and each time the lighting schedule was changed, the timing of ovipositions was completely altered by the fourth day (Morris, 1961; Morris, 1973; Cain and Wilson, 1974; Bhatti and Morris, 1978a).

Circadian rhythms phase-shift in association with the light-dark cycle. Advancement or retardation of the photoschedule has been shown to cause a corresponding shift in the time of ovulation, and hence the open period, as is evident from Figure 2.1. Furthermore, the phase-angle of the open period within a photoschedule is determined by the duration of light and darkness, as shown in Figure 2.2. Figures 2.1 and 2.2 illustrate the relationship between the open period and the light-dark cycle, and thus provide evidence to suggest that the open period possesses circadian characteristics.

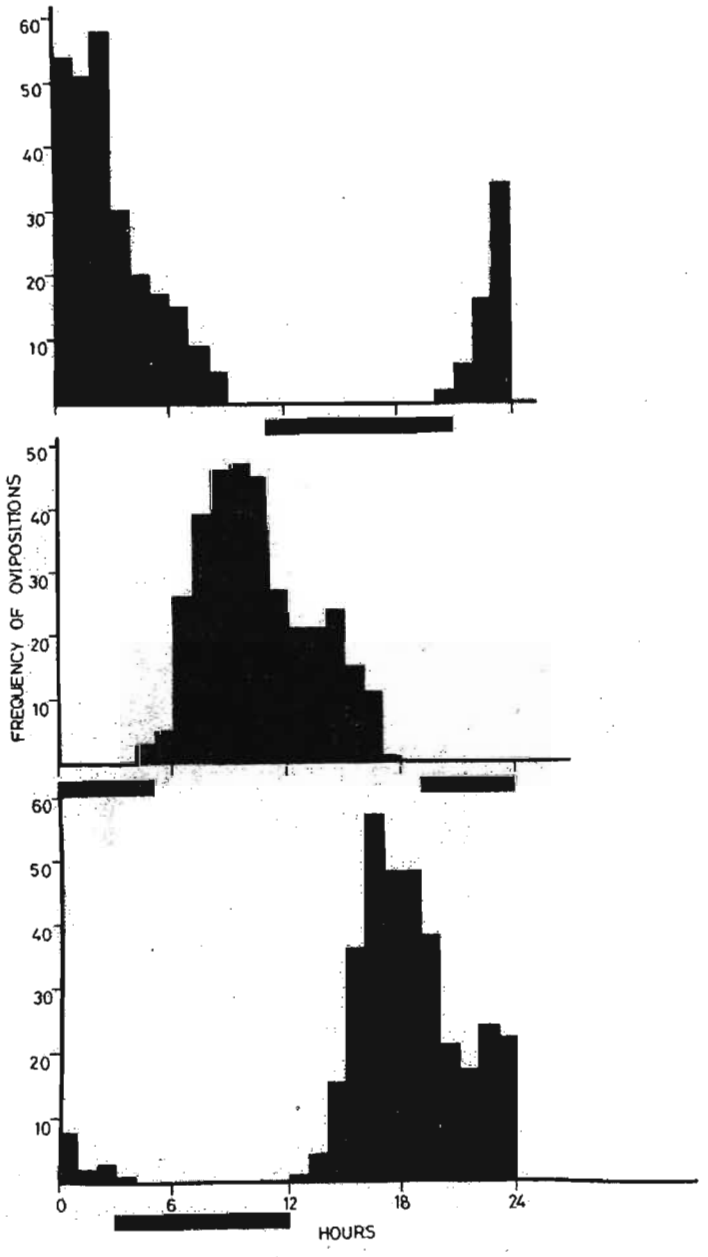

Figure 2.1. *The effect of the time of lights-off in a 14L:10D cycle on oviposition time. The scotoperiod, as indicated by the black horizontal bar, was provided between 12.00 and 22.00 (upper panel), 20.00 and 06.00 (middle panel) or 04h00 and 14h00 (lower panel). From Etches et al. (1984).*

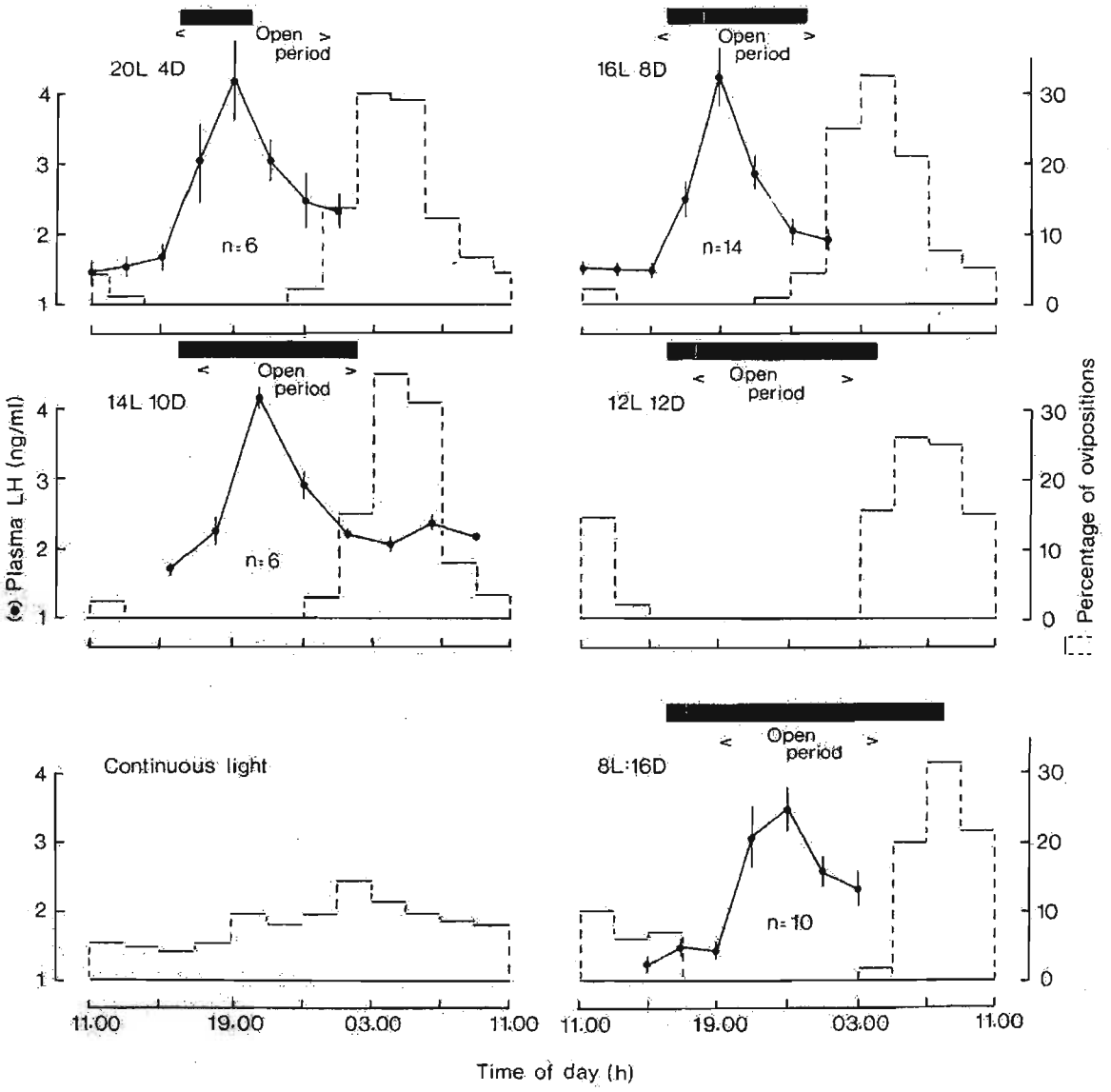

Figure 2.2. *The effect of six photoperiods within a 24 hour cycle on the timing of the first preovulatory LH release of a sequence, and on the distribution of ovipositions. Scotoperiods are represented by the black horizontal bars, and LH concentrations are means ± SE. From Wilson and Cunningham (1984).*

Circadian rhythms are also known to adapt to, or be entrained by, ahemeral (i.e. non-24-hour) light-dark cycles. In experiments such as that shown in Figure 2.3 (Etches *et al.*, 1984), the periodicity of the open period for LH release has been shown to equal the period of the light-dark cycle. Therefore, further evidence to suggest that the open period is the consequence of a circadian rhythm is that the photocontrol of oviposition is affected by the cycle length to

which the birds are exposed (Bhatti, 1987). The primary range of entrainment of oviposition has been found to exist from 21 to 30 hours (Biellier and Ostmann, 1960; Bhatti and Morris, 1978a; Abdulrazik and Morris, 1983; Abdulrazik *et al.*, 1983). When the cycle length is reduced to below 21 hours (Woodard *et al.*, 1962; Davis, 1962; Marks and Lucas, 1963) or increased beyond 30 hours (Biellier and Ostmann, 1960), there is no entrainment, or only partial entrainment of oviposition which resembles oviposition patterns observed under continuous light. Bhatti (1987) stated that entrainment of the open period is further evident in night interruption experiments in which 8 light pulses at hourly intervals in the late subjective night in a 8L:16D photoschedule resulted in the advancement of mean time of oviposition by 3 hours in relation to the onset of dusk in the cycle, as compared with a control treatment without light pulses. Bhatti (1987) attributed this advancement in oviposition time to a "phase advance" effect on the phase response curve underlying the oviposition rhythm, with the 3-hour phase advance presumed to be indicative of the minimum of the primary range of entrainment, i.e. 21 hours.

The third theoretical requirement of a circadian rhythm is that it will free-run in the absence of environmental cues. Numerous authors have attempted to prove that the open period conforms to this requirement by studying oviposition times in either continuous illumination (Warren and Scott, 1936; Lanson, 1960; Morris, 1961; Morris, 1977; Bhatti and Morris, 1977, 1978a; Bhatti, 1987) or continuous darkness (Wilson, 1964). These studies have shown that, although ovipositions occur throughout the 24 hour solar day under constant light or darkness, more ovipositions occur during a modal eight hours of the distribution, as is evident in Figure 2.4 (Etches, 1996a). The unequal distribution of ovipositions throughout the solar day in the absence of the light-dark cycle may be due to hens being able to detect and become entrained to other nocturnal and/or diurnal changes in the physical environment, such as temperature, noise, and feeding cycles (Morris, 1977).

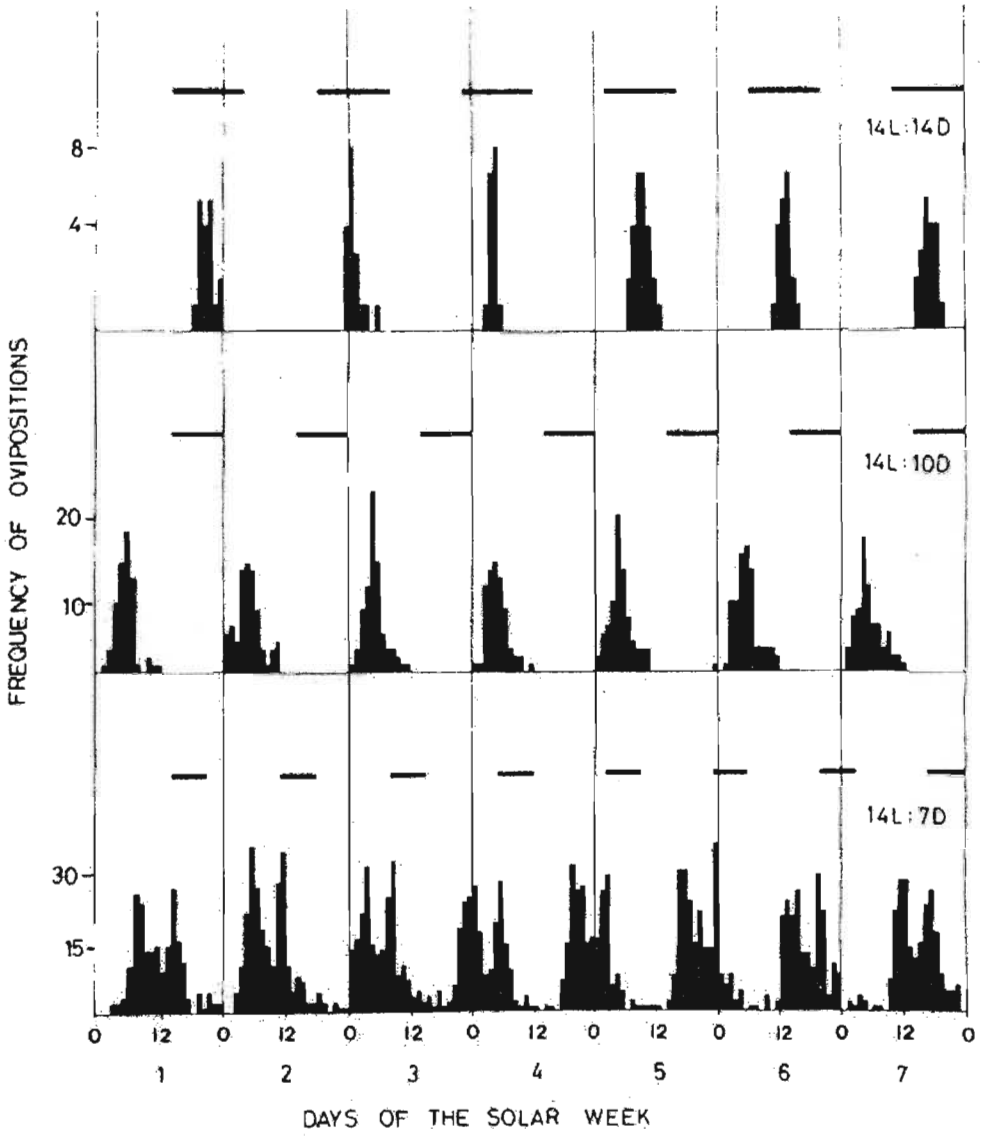

Figure 2.3. *The frequency of ovipositions of hens maintained on a standard 14L:10D photoschedule (middle panel) vs ahemeral light-dark cycles of 14L:14D (top panel) and 14L:7D (bottom panel). From Etches et al. (1984).*

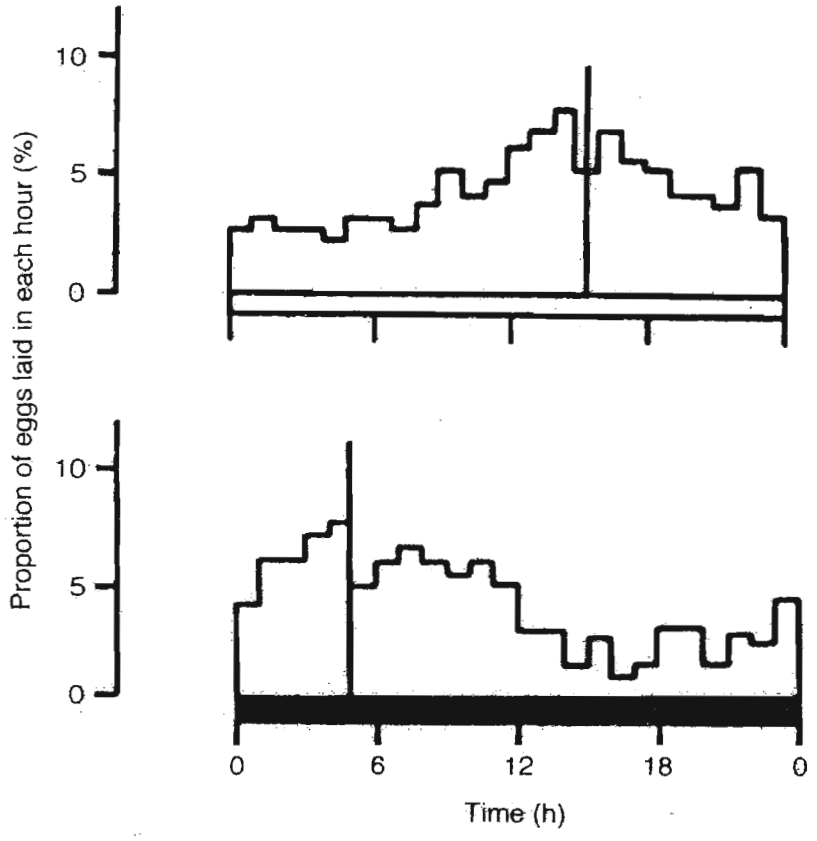

Figure 2.4. *The frequency of ovipositions of hens maintained under continuous light (top panel) or continuous darkness (bottom panel). Ovipositions occur throughout the solar day but 47% and 50% of eggs are laid during the modal 8 hours under continuous illumination and continuous darkness, respectively. If the open period was free-running in such conditions, 33% of eggs should have been laid in each of the three 8 hours of the solar day. The deviations from the expected distribution show that some hens were entrained to subtle cues from the environment, such as sound and temperature. From Bhatti (1987).*

Despite the failure to attribute free-running properties to the open period, other expectations of a circadian rhythm are met by the open period. Due to the general accord between the open period and circadian rhythm theory, a good foundation exists, upon which a theoretical understanding of the ovulatory cycle can be built using principles of circadian rhythms.

2.1.2 The ovulatory cycle

From Table 2.1, it is evident that ovipositions, and hence ovulations, occur in sequences, and are asynchronous due to intervals between intrasequence ovulations, i.e. lag. Therefore, any hypothesis concerning the ovulatory cycle must take into account its asynchronous nature. Fraps (1955) proposed that a threshold exists in some component of the neuroendocrine system which integrates the functional activity of the ovary, hypothalamus and pituitary gland. He postulated a hypothesis in which ovulation is dependent on a circadian rhythm in the sensitivity of a neural component in the ovulatory mechanism to an ovarian excitation factor. This hypothesis accounts for asynchronous ovulation times, and thus intrasequence lag, by proposing that slightly more time than the circadian pacemaker (essentially 24 hours) is required for the F_1 follicle to produce sufficient quantities of the ovarian excitation factor for ovulation.

Neither the neural component, nor the ovarian excitation factor proposed by Fraps (1955) have been identified physiologically. However, the basis of Fraps' hypothesis was used by Etches and Schoch (1984) to produce a mathematical representation of the ovulatory cycle of the domestic hen, which proved accurate in predicting ovulation times in standard and ahemeral photoschedules for sequences of 2 to 9 ovulations, and is consistent with current knowledge of the ovulatory cycle. Johnston and Gous (2003) improved this model so that it could account for age related changes in the ovulation rate of a population of laying hens, and be able to predict the ovulation times for a sequence of any length.

Etches and Scoch's model comprises two equations. The first represents the circadian controlled "regulator of LH release" which causes the preovulatory surge of LH to proceed only during a restricted portion of the solar day. This equation thus represents the open period for LH release. The equation used to describe the changes in concentration or activity of the circadian-related "regulator substance" is a double exponential function similar to that used to describe the increase in the concentration of an injected compound and its subsequent clearance from a biological compartment. The second equation is a Gompertz function which represents a final stage in follicular maturation which is assumed to be initiated when the

previous follicle in the hierarchy is ovulated. Although follicular maturation cannot be precisely defined physiologically, Etches and Schoch (1984) proposed that it may be thought of as the production of the ovarian excitation factor proposed by Fraps (1955) or as an increase in gonadotrophin receptor concentration which might render the follicle sensitive to baseline concentrations of the ovulation-inducing hormone. Etches and Schoch (1984) favoured the latter hypothesis and called this second equation the "receptor function." Ovulation is assumed to occur when a sufficient concentration of the regulator coincides with a sufficient concentration of receptor. The Etches and Schoch model (1984) thus implies that the ovulatory cycle of the hen is not inherently circadian, but rather the result of the interaction of two systems, one of which is regulated by the circadian clock either directly or indirectly. The events of a three-egg sequence, as predicted by this model, are shown in Figure 2.5.

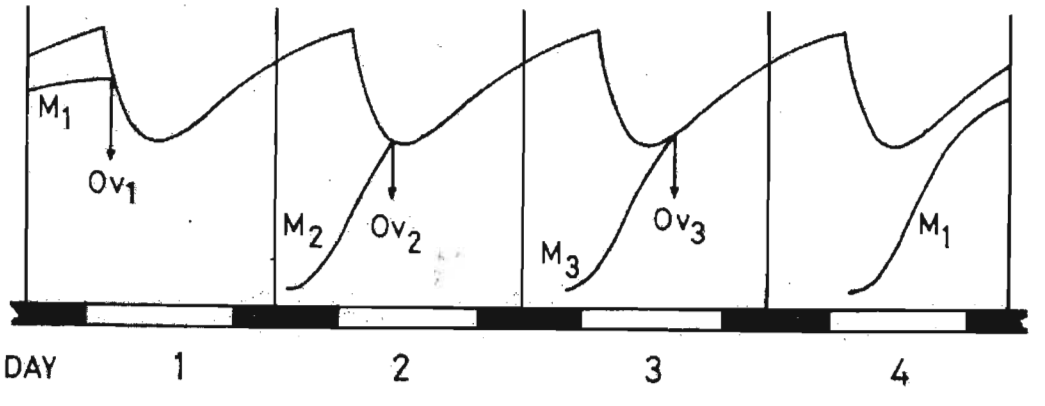

Figure 2.5. *The events of a three-egg sequence as predicted by the Etches and Schoch (1984) model of the ovulatory cycle. The 14L:10D photoschedule is represented by the open and shaded rectangles which span the daily intervals indicated by the vertical lines. The uppermost curve represents the "regulator of LH release," which follows a circadian rhythm and restricts the open period to 8 hours of the day. M_1, M_2 and M_3 represent the maturation of follicles, and their ovulation is indicated at the intersection of the two functions by Ov_1, Ov_2 and Ov_3. From Etches (1984).*

2.1.3 Entrainment of oviposition in light-dark cycles

Various studies have been conducted to determine the role of dawn (lights-on) and dusk (lights-off) in entrainment of oviposition. Warren and Scott (1936) and Biellier and Ostmann (1960) have shown that the time of lights-off in a light-dark cycle is important for the entrainment of oviposition, regardless of cycle length. Lanson (1960) showed that entrainment of oviposition is related to the onset of dusk in photoschedules containing scotoperiods ranging from 0.5 to 10.25 hours offered at different times of the day. The importance of dusk in entraining oviposition has been confirmed by other authors (Wilson, 1964; Wilson *et al.*, 1964; Morris, 1973; Bhatti and Morris, 1977). However, when dusk is either advanced or delayed without altering the time of dawn, the resultant shift in mean time of lay is not equal to the number of hours by which the dusk signal has been displaced (Bhatti and Morris, 1978b). Therefore, dawn has also been shown to exert some influence on oviposition time (Wilson *et al.*, 1964). Naito *et al.* (1980) have suggested that dawn and dusk exert similar effects on the entrainment of oviposition. However, analysis of entrainment of oviposition under the same lighting conditions used by Naito *et al.* (1980) was studied in other experiments (Bhatti and Morris, 1978a, 1988). The conclusions of Naito *et al.* (1980) did not fit with the results of the latter studies, which confirmed that dusk is the more important signal in the entrainment of oviposition. In an experiment reported by Wilson and Cunningham (1984) it was shown that when hens maintained on 16L:8D were transferred to a schedule of 20L:4D in which dawn was advanced by 4 hours, the onset of the open period was advanced, in relation to dusk, by only 30 minutes as judged by mean oviposition time. However, when the 20L:4D schedule was achieved by a 4-hour delay of dusk, the timing of the open period was delayed by 3 hours 8 minutes (Figure 2.6). Dusk was thus, once again, shown to be a more potent signal in entraining oviposition. Care must be taken in deriving conclusions from the above studies as these experiments, aimed at determining the effect of dusk and dawn on oviposition time, were conducted using photoschedules in which the influence of the displaced dawn is inseparable from the consequence of the displaced dusk (Bhatti and Morris, 1978b). This problem was overcome by Bhatti and Morris (1978b) in which entrainment of oviposition was determined for four dusk signals without associated dawns and four dawn signals without associated dusks. Treatments involving single dawns, single dusks and combinations of

dawns and dusks at 12-hour intervals were also tested. It was found that only treatments which included one or more dusk signals gave full entrainment of oviposition. Treatments involving only dawn signals did not fully entrain oviposition but did have some effect on the timing and distribution of ovipositions. Furthermore, dawns given in association with dusks increased the degree of entrainment achieved, when compared with treatments in which the dusk signal was given alone. Bhatti and Morris (1978b) concluded that mean oviposition time under standard light-dark cycles is mainly determined by the time of dusk, but is influenced to some extent by dawn. Therefore, entrainment of oviposition in the hen may be considered to be the result of a complex interaction between the two signals (Bhatti, 1987).

Research on the distribution of ovipositions in short light-dark cycles and skeleton photoperiods has led to interesting findings. Under short light-dark cycles such as 3L:3D or 4L:4D, which are sub-multiples of 24 hours, oviposition is mostly random throughout 24 hours (Duplaix *et al.*, 1981; Nys and Mongin, 1981; Sauveur and Mongin, 1983a). However, under skeleton photoperiods such as 2L:10D:2L:10D, oviposition time is entrained, with most ovipositions occurring in the first 10-hour scotoperiod, with most of these eggs being laid during the first hour of darkness (Mongin, 1980). It has also been shown that skeleton photoperiods using two pulses of light effectively simulate the effects of a continuous photoperiod, only up to a maximum interval of 8 hours between light pulses. When the interval is increased beyond 8 hours, the rhythm of oviposition assume the phase relationship characteristics of the shorter interval (Mian, 1981). Such responses suggest that the open period is entrained by the longest dark period in a cycle. Analysis of responses of oviposition time to intermittent lighting with varying proportions of light and dark in a 24-hour cycle has confirmed this (Mian, 1981).

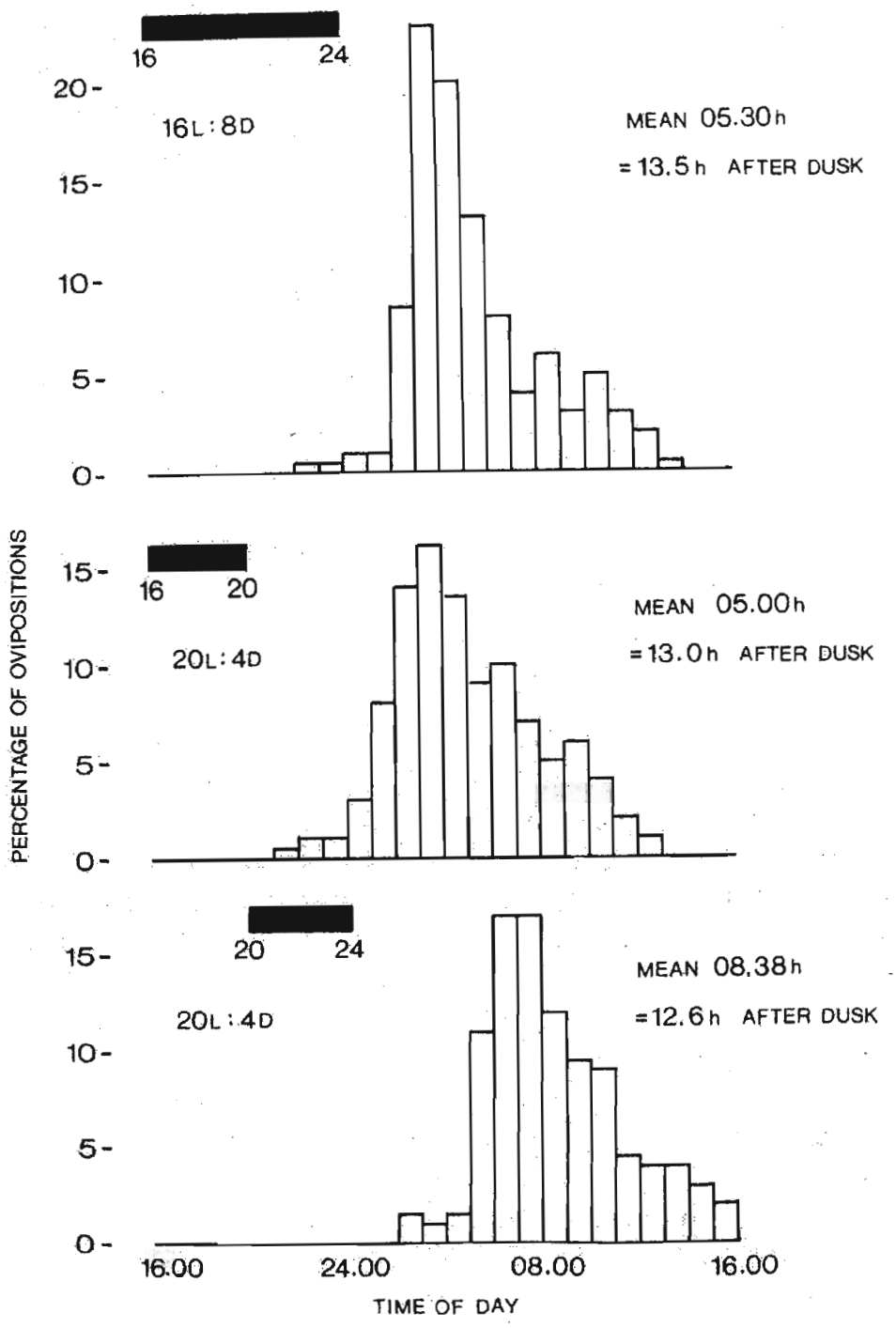

Figure 2.6. *Effect of lengthening the photoperiod from 16L:8D to 20L:4D by advancing dawn (middle panel) or delaying dusk (bottom panel) on the distribution of ovipositions and mean oviposition time. Results during days 8 to 10 after the lighting change are presented. The horizontal black bars represent the scotoperiod. From Wilson and Cunningham (1984).*

Numerous researchers have investigated the minimum signal capable of entraining oviposition. Lanson (1960) reported that a 2.5-hour dark period in a 24-hour photoschedule is the minimum needed for complete entrainment of oviposition, while Cain and Wilson (1974) reported that a minimum 6-hour dark period in a 24-hour cycle is required to produce full entrainment of oviposition. However, neither of these studies made use of an objective measure of entrainment. In an investigation conducted by Bhatti and Morris (1978a), the proportion of eggs laid in a modal 8 hours in a given cycle was used as a suitable measure of entrainment. This study showed that in a 24-hour light-dark cycle, a 15 minute photoperiod or a 5-hour scotoperiod produces essentially the same degree of entrainment as under 6L:18D or 14L:10D photoschedules. The fact that at least 5 hours of darkness is required to achieve full entrainment of the open period probably accounts for the wider distribution of ovipositions in hens on 20L:4D than in hens on a 16L:8D schedule, as shown in Figure 2.6 (Wilson and Cunningham, 1984). Bhatti and Morris (1978a) found that in a 21-hour cycle, full entrainment is achieved with a minimum photoperiod of 3 hours or a minimum scotoperiod of 9 hours, while for a 30-hour cycle, a minimum 8-hour photoperiod or a minimum 12-hour scotoperiod is required for complete entrainment.

2.1.4 Entrainment of oviposition in bright-dim cycles

Circadian rhythms can be synchronised by alternating bright and dim light in a fashion that mimics the light-dark cycle (Bünning, 1967). Morris (1973) found that entrainment of oviposition does not depend upon the absolute level of light intensity, but rather the contrast between the bright and dim phases. This was confirmed by Morris and Bhatti (1978), who determined the role of bright:dim light intensity ratios in the entrainment of oviposition in cycle lengths ranging from 21 to 30 hours, as presented in Figure 2.7. Interestingly, Morris and Bhatti (1978) observed that, for any ratio of bright and dim periods, mean oviposition time is usually advanced in relation to dusk, when compared with corresponding light-dark conditions. Bhatti (1987) attributed this to the phase advance effect, caused by the illumination of late subjective night of the phase response curve presumed to underlay the rhythm of the open period for LH release.

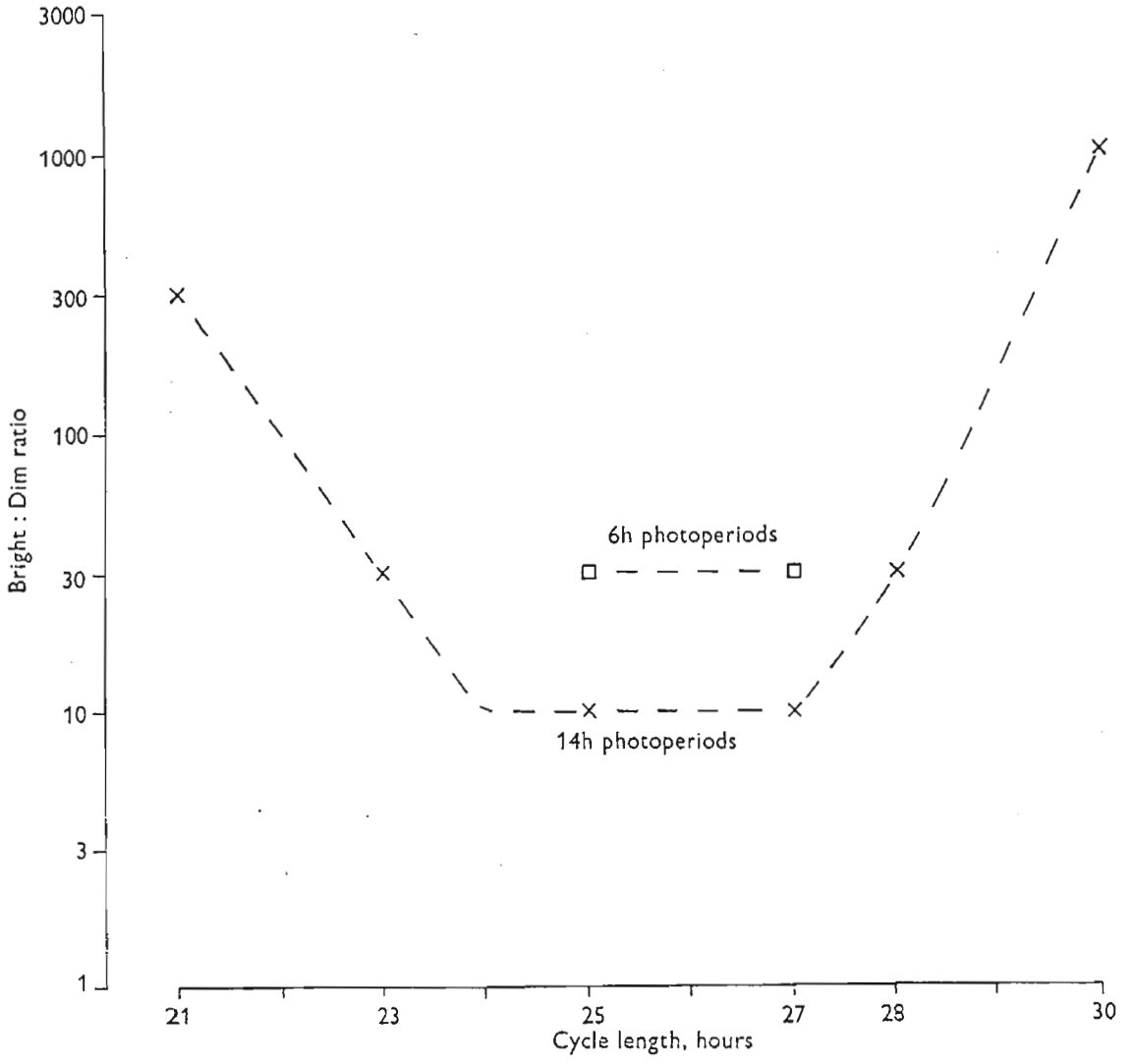

Figure 2.7. *The ratio of bright:dim light intensities required for full entrainment of oviposition in cycles of different lengths. From Morris and Bhatti (1978).*

Research conducted to determine the minimum signal necessary to entrain the open period in bright-dim cycles has shown that, in a 24-hour cycle, one minute of bright light (50 lux) in a background of dim continuous light (0.3 lux) is sufficient to produce complete entrainment of oviposition (Morris and Bhatti, 1978). The minimum dim period required for entrainment of the open period is unknown (Bhatti, 1987). In a 30-hour bright-dim cycle, 8 hours of bright light (26 lux) in combination with 22 hours of dim blue light (0.1 lux) produced complete entrainment of oviposition (Mian, 1981). However, in the same study, 18 hours of bright light (26 Lux) in combination with 12 hours of dim blue light (0.1 lux) resulted in poor entrainment.

Bhatti (1987) stated that these findings imply that the critical ratios between bright and dim light are important when there is modification of the dim lighting period.

In light-dark or bright-dim cycles, the role of dusk in the phase setting of the open period is known, but the relative importance of these types of cycle in a combined system is yet to be determined. However, a comparison of light-dark and bright-dim lighting in 24 hour cycles has shown that the dusk signal associated with the bright-dim regime is a much weaker cue for phase setting oviposition (Bhatti, 1987).

2.1.5 Length of the photoperiod and/or scotoperiod and entrainment of oviposition

It has been established that the length of the photoschedule affects the pattern of oviposition. It has been observed that most ovipositions occur in the scotoperiod when cycle length decreases below 22 hours. When cycle length increases above 24 hours, ovipositions drift into the scotoperiod, and at 27 hours and above, most eggs are laid in the dark (Biellier and Ostmann, 1960; Morris, 1973; Bhatti and Morris, 1978a). An example of the relationship between the distribution of times of oviposition and dusk using conventional or ahemeral photoschedules is given in Figure 2.8. Bhatti and Morris (1988) attributed this change in the pattern of oviposition to the varying phase relationship between dusk and the onset of the open period. This phase relationship has been represented diagrammatically in Figure 2.9.

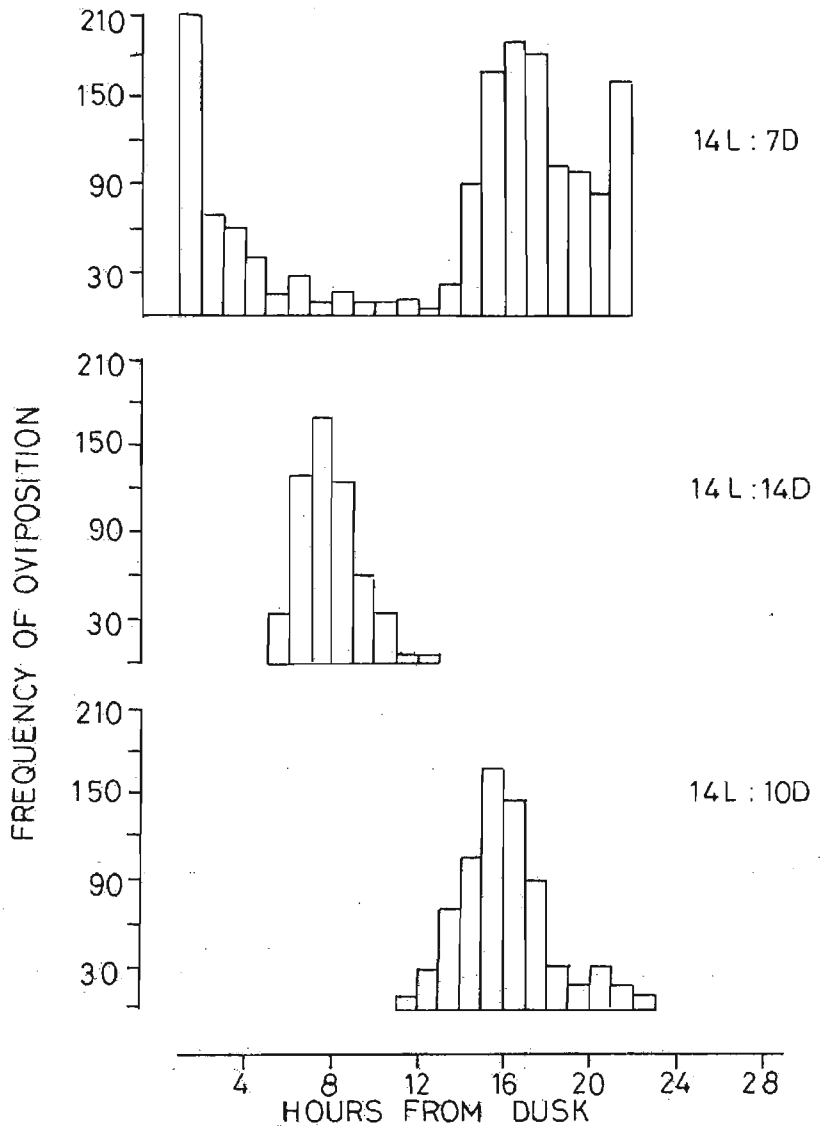

Figure 2.8. *The relationship between the distribution of ovipositions and dusk using standard or ahemeral light-dark cycles. In 14L:7D (upper panel) many eggs are laid during the scotoperiod, and in 14L:14D (middle panel) all eggs are laid in darkness. In the standard 14L:10D cycle (bottom panel), however, the scotophase ends before egg laying starts. From Etches (1990).*

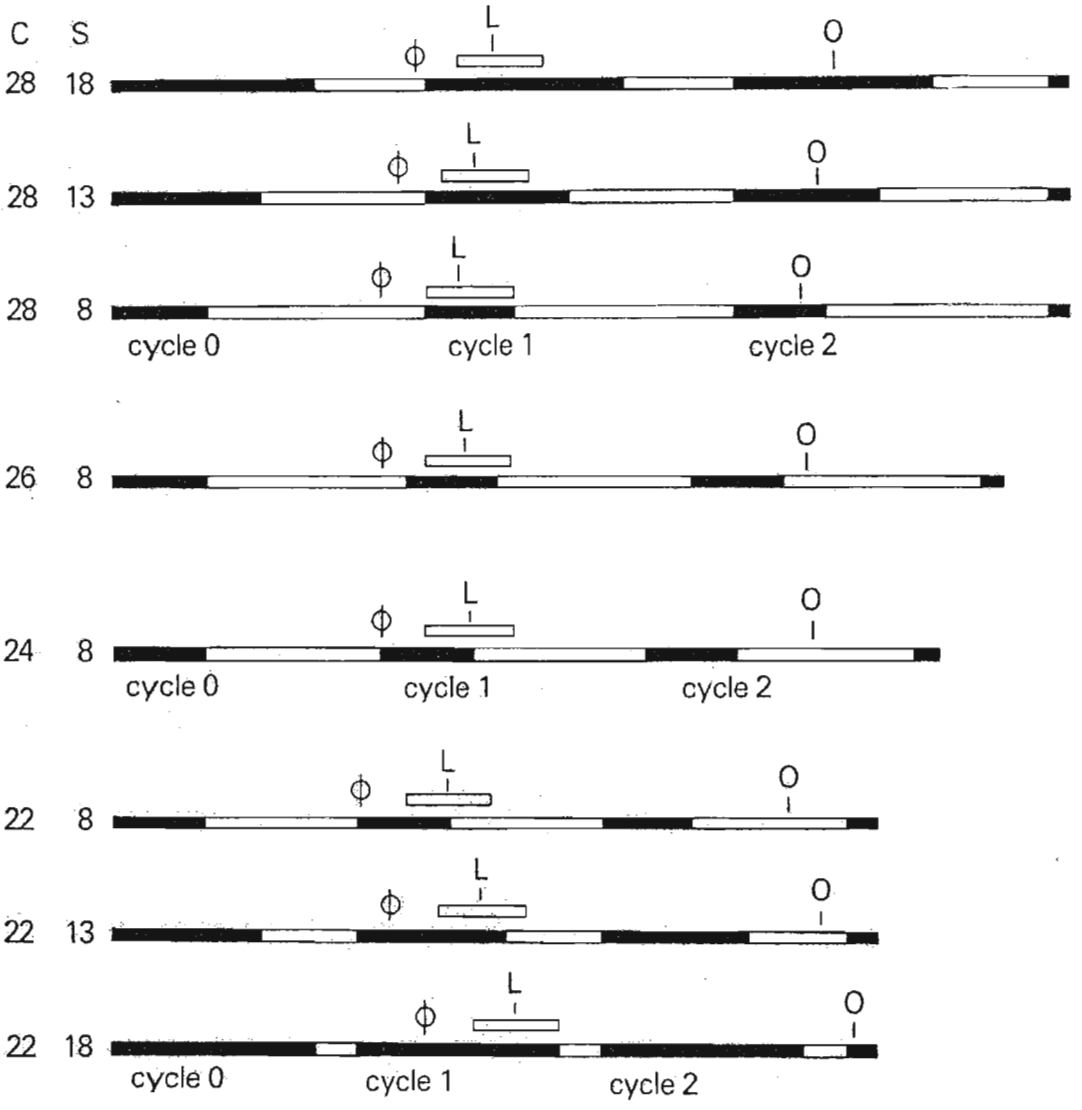

Figure 2.9. *Diagram depicting events in the ovulatory cycle under different light-dark photoschedules. C = cycle length (hours); S = scotoperiod (hours). Solid black bars represent scotoperiods; clear bars represent photoperiods.* O *indicates predicted mean oviposition time in cycle 2. Open rectangles indicate times when maximum plasma concentrations of LH occur, and these correspond, with a time lag of approximately 3 hours to the open periods when LH surges are initiated. L represents the mean time of peak plasma LH concentration (LH releases occur earlier in the open period in 28 hour cycles than in 24 hour cycles). The interval between L and 0 is 31 hours for C = 26 or 28 hours, but 30 hours for C ≤ 24 hours. Ø represents the presumed onset of the subjective night, which determines the timing of the open period for LH release. From Bhatti and Morris (1988).*

From Figure 2.2 and Figure 2.9, it is evident that the timing of the open period is not only affected by the length of the light-dark cycle, but also by the duration of the photoperiod and/or scotoperiod within the cycle. It has been observed that mean oviposition time is different for a schedule of 6L:18D as for 18L:6D (Morris, 1973). Differences in oviposition times have also been observed in 14L:10D *vs* 8L:16D *vs* 19L:5D lighting schedules (Naito *et al.*, 1980). Etches (1990) reported that under standard 14L:10D photoschedules, mean oviposition time is approximately 15 hours after dusk. However, extension or contraction of the scotophase to 18 hours or 6 hours increases or decreases the mean time of oviposition by 4 and 3 hours, respectively. Using data from 26 experiments of light-dark cycles ranging from 21 to 30 hours incorporating various scotoperiods from 5 to 23 hours, Bhatti and Morris (1988) developed a model to predict time of oviposition in most light-dark cycles (Figure 2.10). This model indirectly describes the phase relationship between the open period and dusk, and consists of two equations. The first, which predicts mean oviposition time, in hours from dusk (H), when the light-dark cycle is equal to or longer than 24 hours, is:

$$H = 16.619 - 2(C - 24) - 0.161C + 0.268S \qquad (1)$$

(C = cycle length in hours; S = scotoperiod in hours)

From equation (1), it is evident that time of oviposition is advanced by 2(C–24) for photoschedules longer than 24 hours. Bhatti and Morris (1988) attributed the two periods of lag in the equation to an oviposition in cycle 2 being dependent on an LH release in cycle 1, the timing of which is determined by the onset of dusk at the beginning of cycle 0, as shown in Figure 2.9. The coefficient of the scotoperiod term in the above equation shows that the phase relationship between dusk and the onset of the open period alters by approximately 16 minutes per hour extension of the scotoperiod, or, more practically, a phase delay of one hour is obtained for every 3.7-hour extension of the scotoperiod.

For photoschedules equal to or shorter than 24 hours, the following equation can be used to predict oviposition times:

$$H = 19.026 + (C-24) - 0.260C + (4.482 - 0.175C)S \quad (2)$$

For cycles shorter than 24 hours, dusk occurs in advance of the anticipated ending of the subjective day. This resets the circadian rhythm controlling the open period at or soon after lights out. The open period is then advanced in synchrony with the dusk signal and, thus, using terms relevant to Figure 2.9, it is the lights out at the beginning of cycle 1 which determines oviposition in cycle 2 (Bhatti and Morris, 1988). When comparing the coefficients of the scotoperiod term in equations (1) and (2), it is evident that there is a greater effect associated with changes in scotoperiod within cycles $\leq$ 24 hours, compared with cycles $\geq$ 24 hours. Bhatti and Morris (1988) stated that this difference may be due to the choice of scales used in the formulation of the equations, particularly the scotoperiod being defined in hours. These authors use the following example to illustrate this point. In a 21-hour cycle, a change in scotoperiod from 8 to 20 hours is a proportional change from 0.38 to 0.95 darkness. However, in a 30-hour cycle, the same change in scotoperiod length is only a proportional change from 0.26 to 0.67 darkness. Therefore, it is to be expected that the latter change causes a smaller phase shift in the timing of oviposition. Bhatti and Morris (1988) stated that mean oviposition time with longer scotoperiods in 30-hour cycles, (e.g. a 28.5 hour scotoperiod, which is proportionally 0.95 darkness) cannot be accurately determined, because complete entrainment is not maintained for scotoperiods longer than 22 hours at this cycle length (Bhatti and Morris, 1978a). A re-analysis of the data used to formulate equations based on the ratio of S:C in place of S (hours) was considered, but not attempted. Bhatti and Morris (1988) justified leaving the scotoperiod term as it was, by stating that more accurate predictions using S:C ratios in place of S (hours) seemed unlikely, and that the concept of scotoperiod expressed as a proportion of cycle length may be unfamiliar to potential users of the model. Furthermore, there was doubt as to whether it was statistically correct to assume that C and S:C were independent variables, and thus the use of both these terms in the model may have led to problems of colinearity.

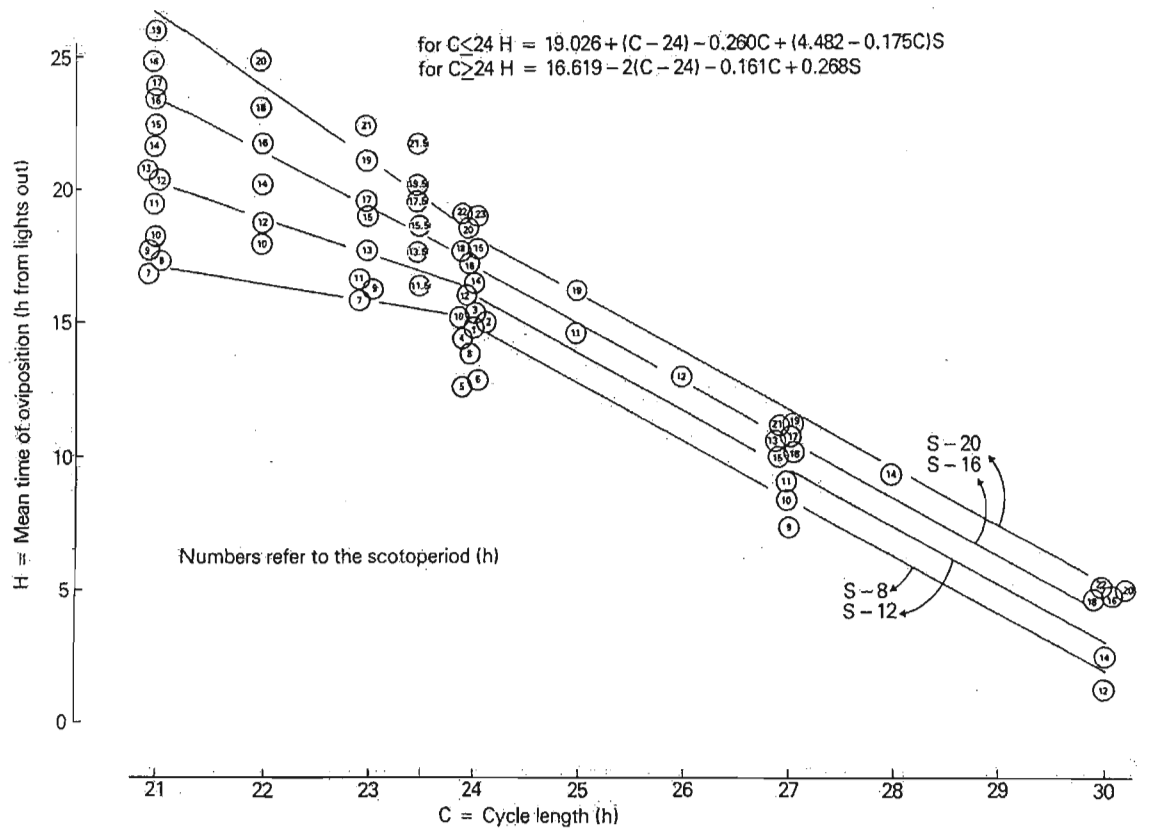

Figure 2.10. *A model for the prediction of mean oviposition time in different light-dark cycles. The model is represented by the straight lines, fitted to data represented by circles. S = scotoperiod (hours) and numbers in the circles give the scotoperiod for that particular data point. From Bhatti and Morris (1988).*

Due to the location of the open period being determined by dawn and dusk, and as the time required for egg formation is relatively constant for a given light-dark cycle, increases in the length of the photoperiod will result in birds laying eggs later in the day (Lewis, 1996). From a regression of oviposition time data derived from mainly white egg-type hybrids, Lewis (1987) reported a 33-minute advance in mean oviposition time (hours post antecedent dusk) per hour increase in photoperiod. Similar findings were reported by Etches (1990), who determined the relationship between the mean time of oviposition and the duration of the scotophase (Figure 2.11).

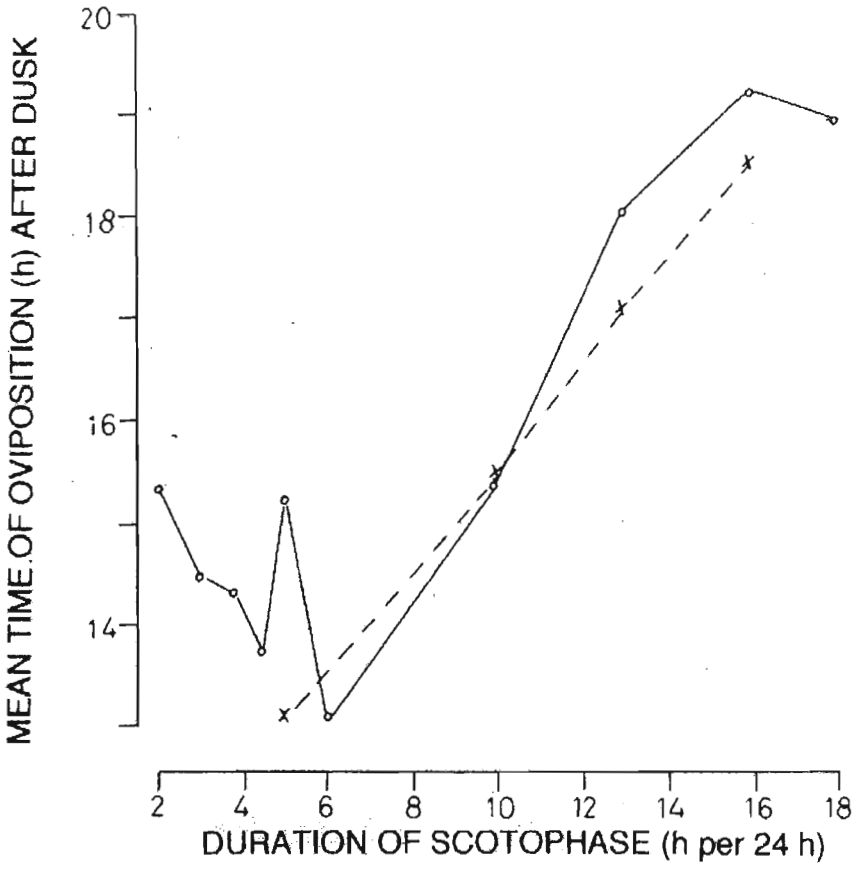

Figure 2.11. *The relationship between the mean time of oviposition following lights-off and the length of the scotophase. From Etches (1990).*

The relationship between photoperiod and oviposition time was again confirmed by Lewis *et al.* (1995) in which oviposition times were studied for brown and white egg-laying hybrids under 8, 10, 13 and 18-hour photoperiods. It was shown that, for both Shaver 288 and ISA Brown egg-type hybrids, although time of lay is different for the different breeds, mean oviposition time is advanced, relative to dusk, by 26-27 minutes per hour increase in photoperiod. Mean oviposition time for the ISA Brown hybrid is 1.2 to 1.4 hours earlier than that of the Shaver 288 hybrid under each lighting regimen. Lewis *et al.* (1995) suggested that a genetic difference in phase setting of the open period for LH release is a likely reason for the difference in mean oviposition time for white and brown hybrids. Other possibilities for the earlier time of lay for the brown-egg hybrid include a shorter egg-formation period, a reduction in the time interval between commencement of the LH surge and its peak plasma

concentration, and a shorter period between peak plasma LH and ovulation (Lewis *et al.*, 1995). Lewis (1987) found no significant differences in mean oviposition time between four genotypes of brown egg-laying hen (Hisex Brown, ISA Brown, Ross Brown and Tetra SL) subjected to either an interrupted or fully illuminated 16L:8D photoschedule. Furthermore, mean oviposition times reported by Lewis (1987), adjusted for photoperiod differences, were similar to those reported by Lewis *et al.* (1995). Therefore, Lewis *et al.* (1995) suggested that the observed differences in time of lay between the Shaver 288 and ISA Brown birds are differences between brown and white egg-laying hybrids generally, rather than differences between these particular breeds of hen.

2.2 PHOTOPERIOD AND EGGSHELL QUALITY

2.2.1 Photoperiod and the incidence of body-checked eggs

Roland and Moore (1980) showed that the incidence of body-checked eggs is significantly influenced by the photoperiod. The incidence of body-checked eggs increased from 7.7% to 18.3% when the photoperiod was increased from 16 to 19 hours. When the photoperiod was reduced back to 16 hours, the incidence of body-checked eggs decreased to 5.8%. A further reduction in photoperiod to 14 hours resulted in a decline in the incidence of body-checked eggs to 1.0%. Therefore, in order to minimize the incidence of body-checked eggs, the photoperiod should not exceed that necessary to ensure maximum egg production (Roland, 1984). The occurrence of body-checked eggs depends on relationships between the photoperiod, hen activity, feeding and a critical period in shell formation, i.e. the first few hours of shell formation when the shell is ultra-thin, which varies directly with ovulation time (Roland, 1984). Roland (1982) suggested that when the critical period of shell deposition occurs during the photoperiod, eggs are more likely to be broken, and become body-checked eggs, than when the critical period occurs during the scotoperiod, due to differences in hen activity. Therefore, manipulations of the lighting schedule to minimize activity at the end of the photoperiod, or during the critical period of shell formation, are also considered to minimize the problem (Roland, 1984).

2.2.2 Photoperiod and eggshell thickness

Two experiments performed by Lewis *et al.* (1994) with ISA Brown and Shaver 288 hybrids showed that eggshell quality of commercial layers is negatively correlated with photoperiod. Shell quality parameters from the two studies are shown in Table 2.2.

Table 2.2. *Mean shell quality parameters for ISA Brown and Shaver 288 birds under different photoperiods. (Lewis et al., 1994).*

Photoperiod (h)	Egg weight (g)	Shell weight (g)	Shell percentage (%)	Shell weight/area (mg/cm^2)
Experiment 1				
ISA Brown				
8	65.0	6.38	9.83	84.5
11	63.5	6.22	9.80	83.5
14	63.0	6.10	9.69	82.4
Experiment 2				
ISA Brown				
8	65.3	6.30	9.71	83.4
10	63.0	6.14	9.76	83.0
13	63.1	6.05	9.63	81.9
16	64.2	6.03	9.47	80.7
Shaver 288				
8	60.4	5.80	9.64	80.7
10	60.4	5.74	9.60	80.2
13	60.6	5.77	9.62	80.6
16	61.4	5.73	9.42	79.2

The following multiple regressions for shell weight, shell percentage, and shell weight per unit area with age and photoperiod were reported:

ISA Brown (Experiments 1 and 2)

Shell weight (g) $= 4.50 - 0.0613P + 0.0827A - 0.000682A^2$

Shell percentage $= 10.4 - 0.0353P + 0.0048A - 0.000158A^2$

Shell weight per area (mg/cm^2) $= 77.9 - 0.475P + 0.419A - 0.00415A^2$

Shaver 288 (Experiment 2)

Shell percentage $= 10.3 - 0.0249P - 0.000148A^2$

Shell weight per area (mg/cm^2) $= 71.6 - 0.166P + 0.509A - 0.00534A^2$

where P = photoperiod (hours) and A = age (weeks)

At present, no explanation has been given for the negative correlation of photoperiod with shell quality. In the study performed by Lewis *et al.* (1994), feed intake increased by 1.25 g per hour increase in photoperiod. As a result, birds on longer photoperiods would have had greater calcium (Ca) intakes. Lewis *et al.* (1994) thus stated that the negative correlation of photoperiod and shell quality is unlikely to be due to nutrition, as shell quality is positively correlated with Ca intake, at least within the range of intakes prevalent in that study. Lewis *et al.* (1994) have also discounted differences in egg weight as a reason for the decline in shell quality, as birds on short photoperiods laid heavier eggs than birds that were subjected to longer photoperiods. Differences in rate of lay were also dismissed as possible causes of differences in shell quality. Lewis *et al.* (1994) suggested that differences in the temporal relationships between the shelling process and feeding, or between hormonal secretions associated with ovulation and shell deposition, may be causal factors.

2.3 FEEDING TIME AND EGGSHELL QUALITY

2.3.1 Calcium metabolism and eggshell formation

The eggshell is comprised mainly of calcium carbonate ($CaCO_3$) crystals, which are made up of Ca^{2+} and CO_3^{2-} ions. The Ca^{2+} ions are obtained primarily from Ca in feed, while CO_2 dissolved in blood is used to synthesize the CO_3^{2-} ions (Simkiss, 1961). During the shell formation period, a supersaturated concentration of Ca^{2+} is maintained in the shell gland fluid to support the precipitation of $CaCO_3$ crystals (Simkiss, 1961). Shell deposition occurs between 8 and 24 hours after the previous oviposition, with maximum shell deposition occurring between 12 and 24 hours after the previous oviposition (Etches, 1996b). The major stage of shell calcification thus occurs during the scotoperiod, when hens do not eat. Due to

the lack of Ca intake during the scotoperiod, Ca^{2+} must be repartitioned during and after absorption to maintain a relatively constant concentration in blood entering the shell gland throughout the period of shell deposition (Etches, 1987). This repartitioning of Ca is made possible by a unique digestive and skeletal system (Simkiss, 1961). The crop stores Ca consumed during the day and meters it to the lower digestive tract at night. In doing so, the passage of calcareous grit through the digestive tract is regulated to optimize the direct utilization of Ca from feed. Furthermore, Ca^{2+} is temporarily stored in bone when the demand for shell formation is low. The storage depots for Ca, which are composed of a labile form of calcium phosphate termed medullary bone, are located primarily in the long bones (Kyes and Potter, 1934). In order to maintain a supply of Ca^{2+} that will support shell calcification, this skeletal Ca is then reabsorbed to the bloodstream during periods when Ca from feed is in short supply.

Calcium metabolism in laying hens, as explained by Etches (1996b), is illustrated in Figure 2.12. The regulation of plasma Ca may be viewed as a control system with three controlling sub-systems – bone, intestine and kidney, and three regulating hormones – parathyroid hormone (PTH), calcitonin (CT) and 1,25-dihydroxycholecalciferol [$1,25(OH)_2D_3$], the biologically active metabolite of vitamin D (Hurwitz *et al.*, 1983). The absorption of Ca^{2+} from the gastrointestinal tract and the release of Ca^{2+} from bone are maximized by the influence of $1,25(OH)_2D_3$. The liver converts dietary vitamin D_3 to 25-hydroxycholecalciferol [$25(OH)D_3$] (Blunt *et al.*, 1968). Stimulated by oestrogens at sexual maturity, the $25(OH)D_3$ is then hydroxylated in the kidney to produce $1,25(OH)_2D_3$ (Fraser and Kodicek, 1970; Holick *et al.*, 1971; Norman *et al.*, 1971), which stimulates absorption of Ca^{2+} from the intestine (Wasserman and Taylor, 1966) and the release of Ca^{2+} from bone (Raisz *et al.*, 1972; Tanaka and DeLuca, 1971). If these two sources of Ca^{2+} are insufficient, the low concentration of Ca^{2+} in the extracellular fluid of the parathyroid gland stimulates the secretion of PTH (Van de Velde *et al.*, 1984). The increased concentration of PTH increases the plasma concentration of Ca^{2+} directly by stimulating osteoclast activity in the bone (Miller, 1978) and indirectly by augmenting the conversion of $25(OH)D_3$ to $1,25(OH)_2D_3$ (Fraser and Kodicek, 1973). The deposition of Ca during shell formation is associated with a decrease in the plasma concentration of Ca^{2+} which results in the release of PTH from the parathyroid glands and,

thus, an increase in the plasma concentration of PTH and $1,25(OH)_2D_3$ to mobilize bone reserves of Ca. Osteoclasts, stimulated by PTH, participate in the mobilization of Ca^{2+} from bone. When the demand for Ca by the shell gland decreases, plasma concentrations of Ca^{2+} increase and the concentration of PTH declines, resulting in a decrease in the activity of the osteoclasts. CT secretion is also stimulated by the hypercalcaemia, resulting, together with the decrease in PTH production, in a diminished bone resorption (Dacke *et al.*, 1976). Mineralisation of the bone matrix increases after oviposition and prior to the formation of the next eggshell (Van de Velde *et al.*, 1985). Thus, the production of the bone matrix during the resorption phase permits the rapid accumulation of Ca into the bone following the completion of shell calcification (Miller, 1992).

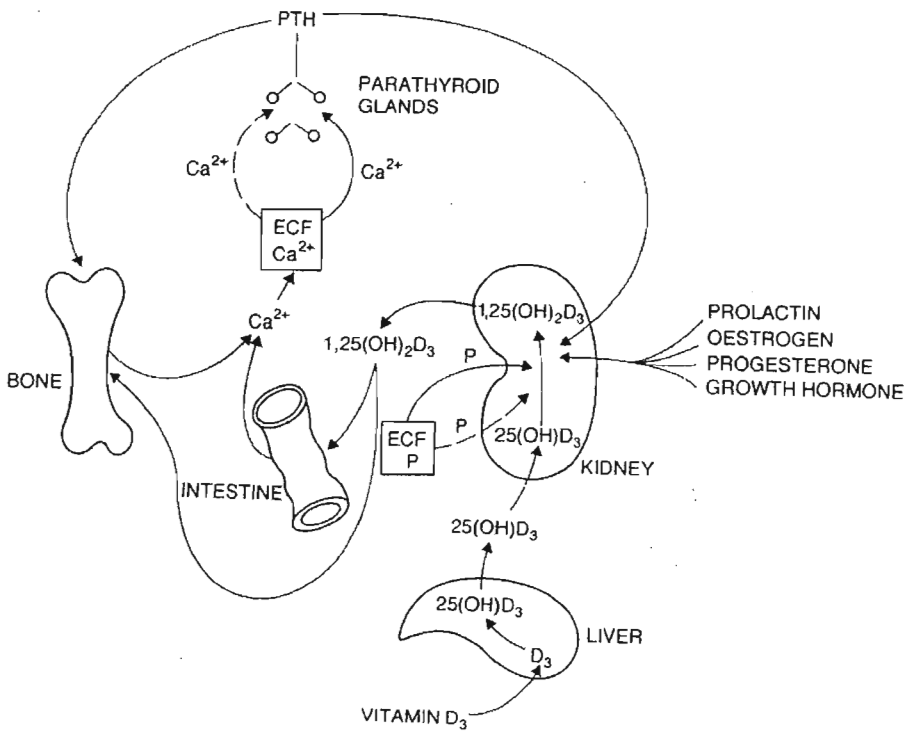

Figure 2.12. *Calcium metabolism in the laying hen. Solid lines represent stimulation and broken lines represent inhibition. Abbreviations are:* Ca^{2+}*, calcium ion; P, phosphorus; and ECF, extracellular fluid. From Etches (1996b).*

The importance of the crop during periods of shell deposition was demonstrated by Voitle *et al.* (1974) and Stonerock *et al.* (1975a, b) who found that cropectomized hens could not

maintain shell quality equivalent to birds with intact crops. This is due to the fact that the crop regulates the flow of dietary Ca to the lower digestive tract throughout the scotoperiod. The metering of Ca from the crop to the lower digestive tract in laying hens is demonstrated in Table 2.3.

Table 2.3. *Feed consumption, dry matter content of the crop, and the concentration of Ca^{2+} in the gizzard at two-hourly intervals throughout the day of laying hens maintained on 14L:10D (lights on at 06.00; lights off at 20.00). (Etches, 1996b)*

Hour of the day	Hours after oviposition	Feed consumption (% of daily feed intake)	Dry matter content of crop (g)	Ca^{2+} content of gizzard (mEq kg^{-1} dry matter)
10.00 - 12.00	2	14	0.6	84
14.00 - 16.00	6	15	1.0	135
18.00 - 20.00	10	17	6.1	205
22.00 - 24.00	14	0	4.4	255
02.00 - 04.00	18	0	4.7	225
06.00 - 08.00	22	10	2.0	156

From Table 2.3, it is evident that feed intake increases two hours before the onset of darkness and that the feed appears to be stored in the crop at the onset of darkness. The feed is then metered to the gastrointestinal tract during the scotoperiod to maximize the delivery of Ca^{2+} to the intestine throughout shell formation (Etches, 1996b). Mongin and Sauveur (1979) showed that bone reabsorption can be reduced by feeding Ca^{2+} as particles that can be identified and specifically consumed by the hen, such as oyster shell or limestone pellets. They found that when given the opportunity to specifically consume Ca, hens consume large quantities of the mineral during the two hours before the onset of the scotoperiod. The crop then acts as a storage depot for Ca, which is released to the lower digestive tract throughout the period of darkness to meet the demands for shell calcification. Since bone is a phosphate salt of Ca in an organic matrix, the plasma concentration of phosphate as well as the organic components of bone, including hydroxyproline, are increased when the release of Ca^{2+} from bone increases (Etches, 1996b). Plasma concentrations of inorganic phosphate (P_i) can thus be used as an index of bone metabolism. Upon analysis of plasma concentrations of P_i, Mongin and Sauveur (1979) found that the nocturnal increase of bone reabsorption is minimised when Ca

is supplied in a particulate form that can be recognised and specifically consumed by the hen. Plasma Ca concentration and plasma P_i levels for hens fed Ca^{2+} as identifiable versus unidentifiable components of feed are shown in Figure 2.13. This figure shows that when compared with hens that receive Ca as an unidentifiable component of the feed, hens that receive Ca as a separate, identifiable component of the diet have higher plasma Ca concentrations and lower plasma P_i concentrations over the period of shell deposition. Mongin and Sauveur (1979) concluded that a separate presentation of dietary Ca reduces bone mobilisation at night. This study further demonstrates the importance of the crop in regulating the flow of Ca to the intestine throughout the scotoperiod, when there is no feed consumption. In doing so, the crop effectively decreases the dependence of shell formation on Ca^{2+} from medullary bone during the scotoperiod.

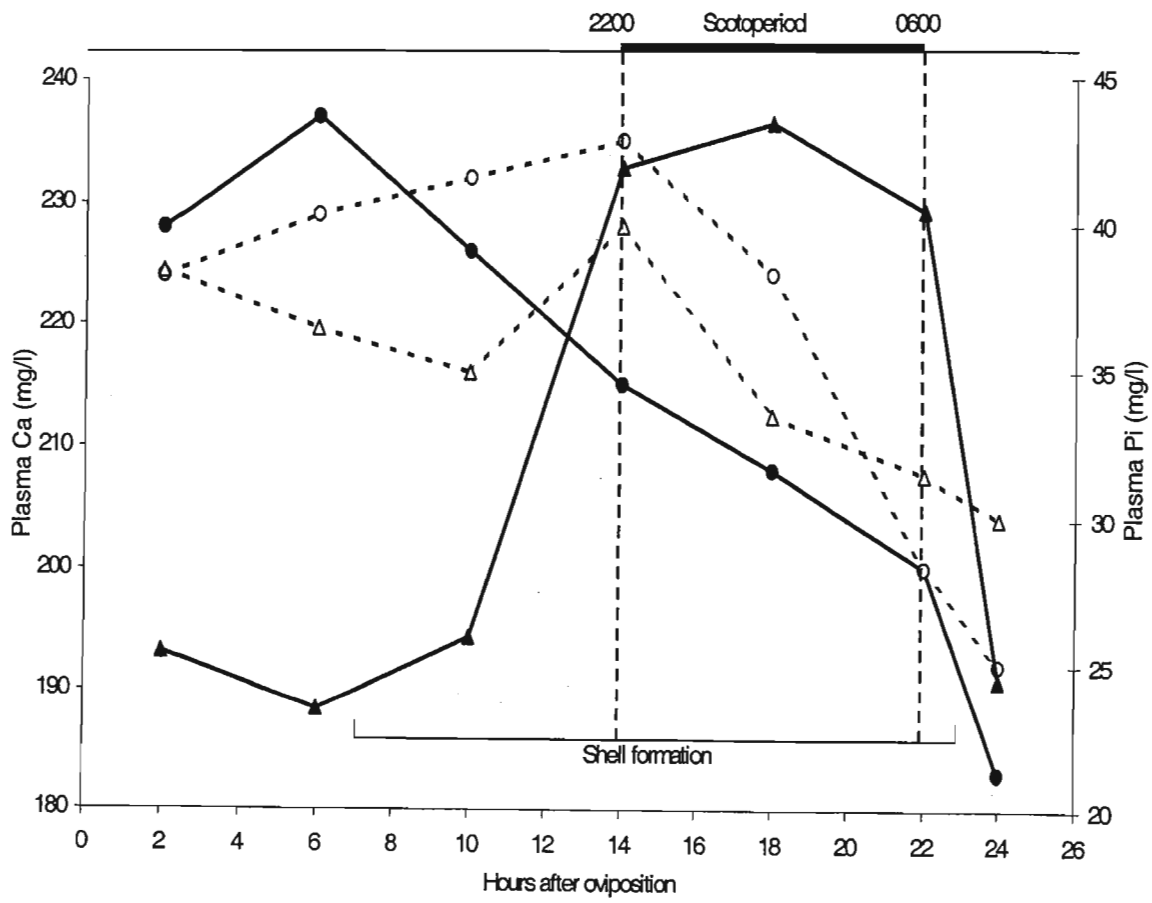

Figure 2.13. *Plasma Ca (circles) and P_i (triangles) concentrations throughout egg formation in hens that are provided with Ca^{2+} as an unidentifiable component of feed (solid line) and as particles, such as oyster shell, that can be specifically consumed (broken lines). Adapted from Mongin and Sauveur (1979).*

The mechanism of bone Ca metabolism is reasonably well understood. What is not as well known is how the bird regulates Ca partitioning between the skeleton and intestine. Utilisation of bone reserves of Ca appears to be initiated when the plasma concentration of Ca^{2+} declines, since Prashad and Edwards (1973) found that reabsorption of bone during shell formation can be prevented experimentally by infusing Ca^{2+} into the vascular system during the period of calcification. However, it is possible that bone mobilisation may be regulated by the Ca status of the small intestine. Sauveur and Mongin (1983b) found a negative relationship between soluble Ca concentration in the duodenum or jejunum and plasma P_i in individual birds in different physiological states. This means that if more dissolved Ca is present in the upper part of the small intestine, less Ca is withdrawn from bone. Therefore, it can be hypothesized that Ca concentration in the upper digestive tract is the signal that regulates bone mobilisation. This hypothesis is corroborated by experimental data (Mongin and Sauveur, 1984). These researchers showed that when individual birds are fed from the previous oviposition on a low Ca diet (1.2% Ca) the immediate response is a large increase in plasma P_i concentration. However, if at 10 hours after oviposition the same birds are intubated with a solution of $CaCl_2$, bone mobilisation, as measured by P_i concentration, is completely blocked even though dietary Ca remains low (Figure 2.14a). On the other hand, if birds are kept on a normal diet (3.5% Ca) and intubated at 10 hours post oviposition with EDTA solution which complexes Ca, plasma P_i concentration rises (Figure 2.14b).

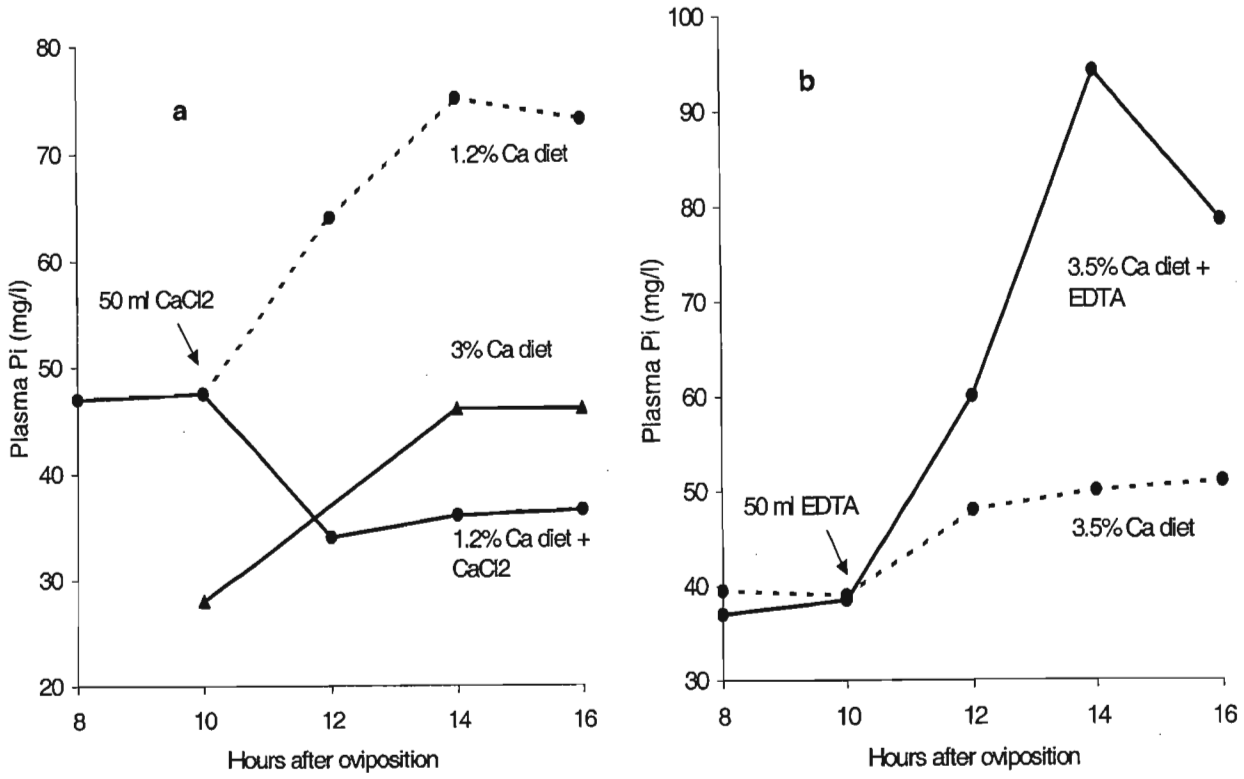

Figure 2.14. *Influence of gastrointestinal status of Ca on the plasma P_i concentration. (a) Effect of a low Ca diet (1.2%) with or without intubation of $CaCl_2$ at 10 hours after oviposition as compared with a normal Ca diet (3%). (b) Effect of intubation of EDTA at 10 hours after oviposition on birds fed a normal Ca diet (3%). Adapted from Mongin and Sauveur (1984).*

2.3.2 Time of calcium intake and eggshell quality

Due to its role in regulating bone mobilisation, dietary Ca availability has a large influence on the shell formation process and hence eggshell thickness. The availability of Ca for eggshell deposition depends not only on the form and concentration of Ca in the diet, but also on the time of Ca intake. The influence of timing of Ca intake on eggshell quality was demonstrated by Lennards and Roland (1981). In this study, three groups of laying hens were fed differently with regards to the time of Ca intake. A control group was fed a 3.4% Ca diet from 06.00 to 20.00 daily. The other two groups were fed a 0.4% Ca diet over the same period and were intubated with 3 g of Ca at either 08.00 or 20.00 daily. Although total Ca intake was the same

for all three groups, the hens intubated with Ca at 08.00 could not maintain egg specific gravity or shell weight at levels comparable to that of the controls. The hens intubated with Ca at 20.00 did, however, have shell weight and specific gravity levels equivalent to the controls. Lennards and Roland (1981) concluded that time of Ca intake is important for shell deposition and that the most important time for hens to receive Ca is during the afternoon.

If the timing of Ca intake is important with regard to shell formation in laying hens, which are fed *ad libitum*, problems of Ca deficiency during shell formation will be exacerbated in broiler breeder hens. This is due to the fact that broiler breeder hens are fed a limited amount of feed per day, and normally consume their daily feed allocation in the first two to six hours of the morning (Roland and Farmer, 1984).

Farmer *et al.* (1983a) performed a study to determine the status of the gastrointestinal tract of the broiler breeder over a 24-hour period. Hens were restricted to four hours of feeding time and then killed at zero, three, 12, 15 and 20 hours after the end of the feeding period. At the end of the feeding period, one half of the feed consumed remained in the digestive tract. By three hours after feeding, only one third of the feed remained in the digestive tract. The pattern of flow of feed through the digestive tract was similar for the crop, with most of the feed passing through the crop by three hours after the end of feeding. This study showed that broiler breeders were similar to laying hens in that they could not maintain a constant or equal rate of flow of feed through the digestive tract throughout a 24-hour period.

Farmer *et al.* (1983c) performed an experiment in order to determine the importance of the time of Ca intake on broiler breeder eggshell quality. Three groups of broiler breeder hens were used. The first group was a control treatment where birds were fed a 3.1% Ca diet. The other groups were fed the same diet, except that it contained only 0.4% Ca and birds were intubated with 3g Ca at either 08.00 or 16.00 daily. All hens received the same total amount of calcium. Results showed that egg specific gravity was adversely affected in hens intubated at 08.00 when compared with controls, while hens intubated at 16.00 showed no drop in egg specific gravity. Farmer *et al.* (1983c) thus showed that the time of Ca intake is an important

factor in shell formation in broiler breeders, and that, to maximize shell quality, the most important time for hens to receive Ca was during the afternoon.

Due to the importance of feeding time with respect to shell formation, Farmer *et al.* (1983c) performed an experiment to further clarify the effects of AM- *vs.* PM-feeding on eggshell quality. Broiler breeder hens were fed a 3.0% Ca diet during one of two feeding periods, i.e. 07.00 – 09.30 (AM feeding) or 15.30 – 18.00 (PM feeding). At the end of the feeding trial, hens were killed at various intervals during a 24 hr period and the Ca and dry matter contents of the digestive system determined. It was found that the flow of feed through the digestive tract was similar for both the AM and PM treatments. If an exponential curve is fitted to the data reported in this study, the following regression equation of percentage Ca remaining in the gastrointestinal tract (y) *vs* number of hours after the start of feeding (x) is obtained:

$$y = 9.74 + 86.11\ (e^{-0.153\ x})$$

The observed means (Farmer *et al.*, 1983c) and fitted line are shown in Figure 2.15.

Although the flow of feed through the digestive tract was the same for AM- and PM-fed hens, there were differences in the Ca status of the digestive system in relation to the initiation of shell calcification between treatments, with PM-fed hens having significantly more Ca available than AM-fed hens during the stages of eggshell calcification. Due to the higher availability of Ca, Farmer *et al.* (1983c) found that shell quality in PM-fed hens is significantly better than in AM-fed hens, thereby confirming the results of previous studies.

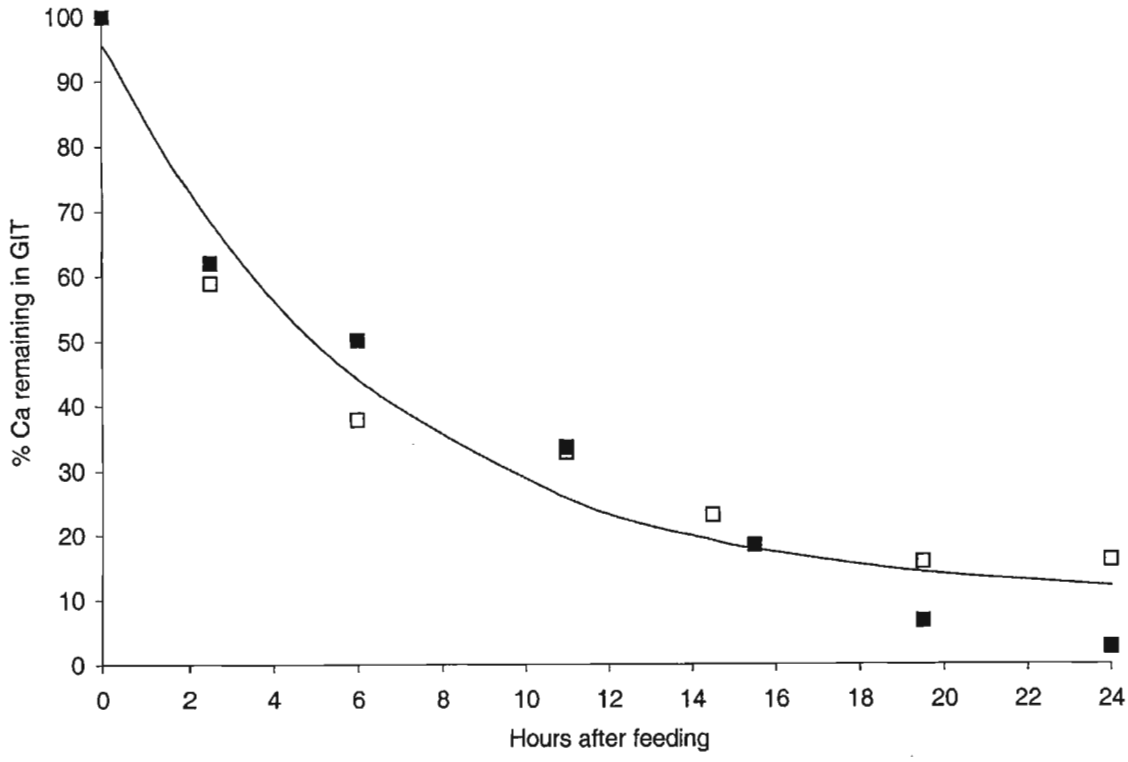

Figure 2.15. *Percentage Ca remaining in the gastrointestinal tract (GIT) vs the number of hours after feeding for AM- (□) and PM-fed (■) broiler breeder hens. Data from Farmer et al. (1983c).*

2.3.3 Mechanism for calcium utilisation

Roland and Farmer (1984) proposed the following hypothesis to explain the positive effect of delayed feeding on broiler breeder eggshell quality. In morning fed birds, most of the Ca passes through the digestive tract before the initiation of shell calcification. These hens have to store most of the Ca in the bone and, therefore, the route Ca takes to the eggshell for morning fed birds is via the small intestine to blood to bone to shell gland and eventually to shell. However, hens fed in the afternoon, at the commencement of shell deposition, could deposit the Ca directly on the egg via the blood, and bypass the bone. Roland and Farmer (1984) stated that if this mechanism is correct, then more skeletal Ca should be present in eggshells from morning fed birds than from birds fed in the afternoon. This would result in decreased shell quality in morning fed hens due to the negative correlation that exists between bone mobilisation and eggshell weight (Sauveur and Mongin, 1983b). Studies with

radioactive ^{45}Ca (Farmer and Roland, 1983; Farmer *et al.*, 1983b, 1986) showed that this is indeed the case, i.e. skeletal Ca is inversely related to the availability of dietary Ca, and the greater the percentage of skeletal Ca used in shell calcification, the poorer the shell quality.

2.3.4 Calcium supplementation via free choice feeding

Farmer and Roland (1982) performed an experiment to determine whether $CaCO_3$ could be fed free choice to broiler breeder hens in the afternoon in order to correct the Ca deficiency at night, instead of feeding a complete meal. It was found that in order to maximize shell quality, broiler breeder hens not only need Ca but also feed with the Ca. The results suggested that broiler breeder hens cannot absorb Ca efficiently from the digestive tract or mobilize skeletal Ca when other nutrients, such as vitamin D_3 and phosphorus, are lacking in the digestive system. Farmer and Roland (1982) concluded that free choice feeding large particles of $CaCO_3$ to breeders in the afternoon is only partially effective in supplying additional Ca at night for shell calcification.

2.3.5 Feeding time and broiler breeder performance

Due to the relationship of feeding time and shell formation, numerous studies have been performed to determine the effect of different feeding times on broiler breeder performance. Bootwalla *et al.* (1983), Farmer *et al.* (1983c), Brake (1988) and Harms (1991) reported increases in egg specific gravity when birds were fed later in the day. Lewis and Perry (1988) reported an increase in shell thickness and shell weight when broiler breeders were fed half the daily food allocation twice daily compared to a single allocation of food provided in the morning. However, there are some contradictions, such as experiments performed by Brake (1985), Wilson and Keeling (1991), and Samara *et al.* (1996), in which no effects of time of feeding on eggshell quality were observed.

There is also contention in the literature with regard to the effect of feeding time on rate of lay. Brake and Peebles (1986) and Harms (1991) observed a decline in egg production when feeding time was changed from morning to afternoon, whereas others found no adverse effects

of afternoon feeding on egg production (Bootwalla *et al.*, 1983; Brake, 1988; Wilson and Keeling, 1991; Samara *et al.*, 1996).

2.4 FEEDING TIME AND OVIPOSITION TIME

Although afternoon feeding of broiler breeders may result in improved shell quality, there is a potential concern, substantiated by subjective commercial observations (Lewis and Perry, 1988), that delaying the time of feeding may result in delayed oviposition times. Such delays may cause egg collection problems in that a larger proportion of eggs may be laid late in the afternoon or in the early evening, after the final egg collection of the day. Various researchers have attempted to determine whether changing the time of feeding alters the distribution of ovipositions throughout the day. However, results are contradictory. Harms (1991) and Samara *et al.* (1996) reported a delay in the time of oviposition when broiler breeders were fed later in the day. A similar response was observed in cross-bred layers (Daniel and Balnave, 1981) and Japanese quail (Hassan *et al.*, 2003). However, no difference in oviposition times was observed between morning- and afternoon-fed breeders (Brake,1985) or between broiler breeders fed a single allocation of food in the morning or half the daily food allocation twice a day (Lewis and Perry, 1988). On the contrary, Wilson and Keeling (1991) reported a delay in oviposition time due to afternoon feeding in standard sized broiler breeders, but observed no such response in dwarf breeders.

2.5 THE NEED FOR FURTHER RESEARCH

The aim of this chapter was to review the literature pertaining to the effect of photoperiod and feeding time on oviposition time and eggshell quality of the domestic fowl.

Previous research has shown that daylength, in particular the transition from day to night, exerts a powerful influence on the timing of the preovulatory release of luteinising hormone in domestic hens and, in turn, the time of oviposition. The influence of the length of the photoperiod on the time of oviposition has been extensively studied in laying-type hybrids. There is, however, a dearth of information on the effect of photoperiod on oviposition time for

control-fed broiler breeders. This lack of knowledge alone makes research in this field worthwhile. Furthermore, due to oviposition time being of importance in commercial broiler breeder operations with regard to egg collection and grading, such research is of practical relevance.

Eggshell thickness of laying-type hybrids is negatively correlated with photoperiod. Such a relationship has not been studied in control-fed broiler breeders. Reduced shell quality can adversely affect fecundity, with thinner shells being associated with reduced hatchability, and increased embryonic mortality (McDaniel *et al.*, 1981; Roque and Soares, 1994). A study of the effect of photoperiod on broiler breeder eggshell quality is thus necessary, particularly because many broiler breeder producers provide birds with photoperiods in excess of that required for maximum egg production.

The effect of feeding time on oviposition time and eggshell quality of broiler breeders has been reported. However, as results in the literature are contradictory, more research is needed to establish firm conclusions.

CHAPTER 3 *

THE EFFECT OF PHOTOPERIOD ON OVIPOSITION TIME OF BROILER BREEDERS

3.1 INTRODUCTION

Daylength, in particular the transition from day to night (dusk), exerts a powerful influence on the timing of the preovulatory release of luteinising hormone (LH) in domestic hens and, in turn, the time of egg-laying (Bhatti and Morris, 1978a). However, not all breeds of fowl lay their eggs at the same time when given a common daylength; for example, egg-laying in brown-egg hybrids is consistently about 1.5-h earlier than white-egg hybrids (Lewis, 1987; Lewis *et al.*, 1995). A genetic difference in the phase setting of the open period for LH release is thought to be the likely reason for this disparity. In contrast, both types of fowl exhibit a similar rate of change in oviposition time for a given change in photoperiod (Lewis *et al.*, 1995).

There is, however, a dearth of information on the effect of photoperiod on oviposition time for control-fed broiler breeders. This chapter reports the findings of two experiments in which the oviposition time of broiler breeders was measured for photoperiods ranging from 8 to 16 h.

3.2 MATERIALS AND METHODS

The first experiment involved a nominal 3200 Cobb '500' broiler breeder hens housed on the floor in 8 light-proof rooms, each room comprising 4 pens of 100 females (and 10 males). Light was provided by a single 100W incandescent lamp located at a height of 2.2 m in the centre of each pen, resulting in a mean light intensity of 25 ± 4.4 lux at a height of 40 cm. Photoperiods within a 24-h cycle were 10, 11 (2 rooms), 12 (2 rooms), 13, 14 or 16 h, and all started at 07.00. Subsequent to all eggs being cleared on the preceding evening, egg-

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collections were conducted continuously from 04.30 until egg-laying had finished at 18.30 (times determined by a preliminary investigation) for 1 d at 33 weeks of age. The second experiment used the same genotype, but with 60 hens housed in individual cages in each of two light-proof rooms; one room on 8-h and the other on 16-h photoperiods. Light was provided by two 100W incandescent lamps, with mean light intensities of 110 ± 7.0, 60 ± 3.3 and 34 ± 1.8 lux at the feed trough of the top, middle and bottom tier of cages, respectively. As in the first experiment, eggs were cleared on the preceding evenings, and collections made continuously throughout each day's egg-laying period. Six collections were made over three 2-d periods during the 37th and 38th weeks of age. Oviposition times for hens in the second experiment were later than for those in the first experiment because age-related increases in egg weight cause egg-laying to be progressively delayed as hens age (Lewis and Perry, 1991). This difference was removed by fitting a constant to the Experiment 2 data by least squares. Data for the proportion of eggs laid before dawn were divided into two sets with regression lines fitted above and below a hinge point, as described by Lewis *et al.* (1998). The hinge point was found by iteration at 0.25-h intervals to identify the model that minimised the residual sums of squares about the fitted model.

3.3 RESULTS AND DISCUSSION

Mean oviposition time and time when half the day's eggs had been laid (relative to dawn) for the various photoperiods are given in Table 3.1. Figure 3.1 illustrates the relationship between mean oviposition time (relative to the antecedent dusk) and length of the photoperiod. The proportion of eggs laid before the dawn of various photoperiods are shown in Figure 3.2. The length of the complete ovulatory cycle from the beginning of the surge in luteinising hormone (LH) release to the resulting oviposition is about 35 h (Lewis, 1987), and so the zeitgeber for the preovulatory LH release that initiates an ovulation is not the light-dark interface that immediately precedes an oviposition, but the one that occurred 24 h before that (initiating dusk). Therefore, for physiological correctness, regression equations in this chapter are expressed and Figure 3.1 drawn using the initiating dusk as the reference point. However, to facilitate practical use, data in Table 3.1 and Figure 3.2 have been referenced to the start of the photoperiod in which the eggs were laid. It should be noted that as photoperiod is extended,

oviposition times are advanced relative to dusk, but delayed relative to dawn. For example, if mean oviposition time occurs at 09.00 for hens given an 11-h photoperiod from 06.00 to 17.00, and at 10.00 for birds given a 13-h photoperiod from 06.00 to 19.00, the laying of the latter birds is delayed by 1 h relative to dawn (+4 h compared with +3 h), but advanced by 1 h relative to dusk (+15 h compared with +16 h). Obviously when referenced to the initiating dusk, these figures become +39 h compared with +40 h respectively.

Table 3.1. *Mean oviposition time and time when 50% of eggs had been laid (h.min) relative to the start of the photoperiod in which the oviposition occurred for broiler breeder hens given various photoperiods.*

Photoperiod (h)	Mean oviposition time	50% eggs laid
Experiment 1		
10	2.42 ± 0.08	2.25 ± 0.07
11	3.21 ± 0.06	3.00 ± 0.05
12	3.49 ± 0.07	3.37 ± 0.07
13	4.16 ± 0.06	4.08 ± 0.13
14	5.00 ± 0.10	4.48 ± 0.10
16	5.03 ± 0.01	5.27 ± 0.10
Experiment 2		
8	2.44 ± 0.19 (1.52)[1]	2.27 ± 0.23 (2.03)[1]
16	5.57 ± 0.05 (5.05)[1]	5.32 ± 0.02 (5.08)[1]

[1] Means adjusted by least squares for differences from Experiment 1 in parentheses.

A regression of mean oviposition time (using daylengths of ≤ 14 h, and adjusted data for Experiment 2) on photoperiod showed that it was advanced by about 0.5 h for each 1-h extension of the photoperiod between 8 and 14 h relative to the initiating dusk (but delayed by 0.5 h relative to the current dawn).

$y = 45.7 - 0.485p$ ($P<0.001$, $r^2 = 0.990$, Slope SE = 0.020, SD = 0.096)

where y = mean oviposition time (h relative to the initiating dusk), and p = ≤ 14-h photoperiod (h). Mean oviposition times were similar for 14 and 16-h photoperiods, at about 5 h after dawn (Table 3.1). In contrast, the time at which half of the day's eggs had been laid continued to

advance by about 0.5 h/h, relative to the initiating dusk throughout the range of photoperiods tested. The equation describing the regression was:

$y = 46.3 - 0.555p$ ($P<0.001$, $r^2 = 0.981$, Slope SE = 0.030, SD = 0.227)

where y = time when half a day's eggs have been laid (h relative to the initiating dusk), and p = photoperiod (h).

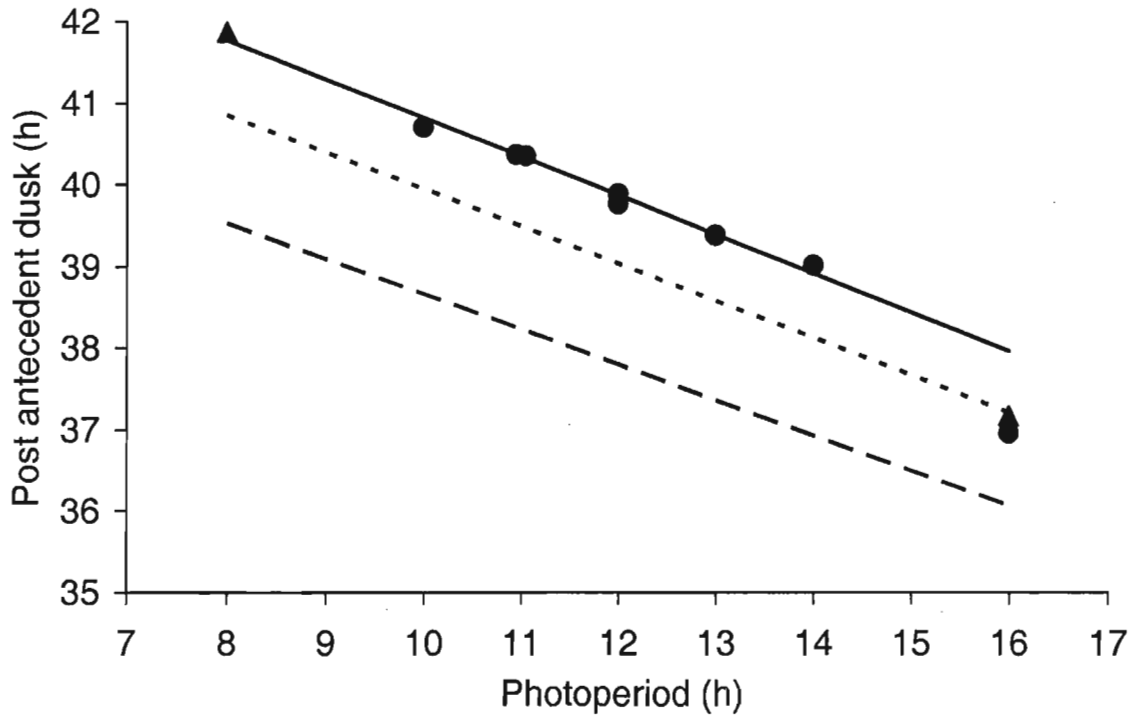

Figure 3.1. *Mean oviposition time relative to the antecedent dusk for Cobb 500 broiler breeder hens maintained on various photoperiods (● Experiment 1, ▲ adjusted Experiment 2); the solid line represents the regression for photoperiods between 8 and 14 h. The dashed line represents a regression for ISA Brown brown-egg hybrids and the dotted line a regression for Shaver 288 white-egg hybrids (from Lewis et al., 1995).*

Under short daylengths, some eggs are laid before the start of the photoperiod (Figure 3.2). A 'hinge' analysis indicated that the number of eggs laid before dawn will be minimised by providing a photoperiod of $\geq$ 12.25 h and, for daylengths shorter than this, numbers will increase by about 0.045 for each 1-h reduction in photoperiod. The regressions were described by the equations:

For photoperiods ≤ 12.25 h: $y = 0.5784 - 0.0457p$ (Slope SE = 0.0089)

For photoperiods ≥ 12.25 h: $y = 0.0235 - 0.0004p$ (Slope SE = 0.0155)

Overall regression: P=0.004, $r^2 = 0.916$

where y = proportion of eggs laid before dawn, and p = photoperiod (h). The change in the proportion of eggs laid before dawn for photoperiods between 12.25 and 16 h is negligible and for practical purposes can be regarded as being constant at less than 0.01.

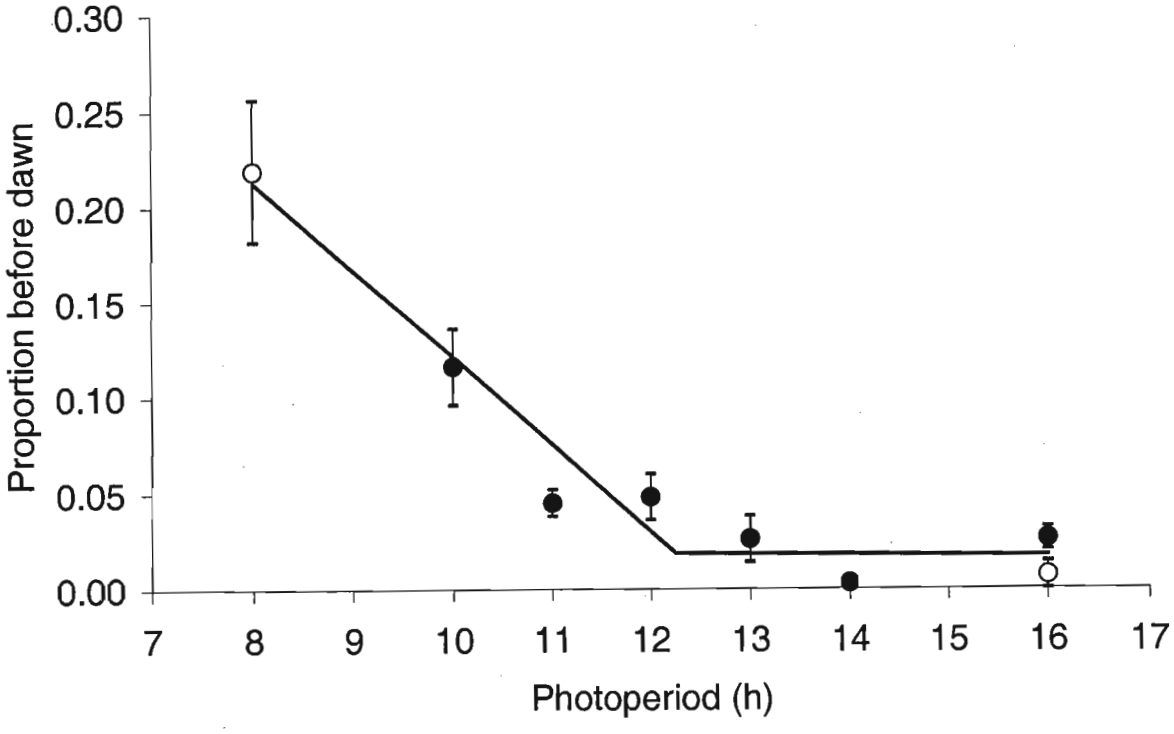

Figure 3.2. *The proportion of eggs laid before the dawn of various photoperiods by Cobb 500 broiler breeder hens (●* = Experiment 1, ○ = Experiment 2*), with SEMs indicated by vertical bars.*

The -0.485 h/h estimated rate of change in oviposition time relative to the initiating dusk with increasing photoperiod compares remarkably well with regression slopes of -0.434 (ISA Brown) and -0.456 (Shaver 288) reported by Lewis *et al.* (1995), -0.546 (various white-egg hybrids) from Lewis (1987), and -0.495 (unknown genotype) from Etches (1990). The equation constant, however, shows that for a given photoperiod mean oviposition time was

about 1 h later than Shaver 288, 2.5 h later than ISA Brown (Figure 3.1), but similar to the historical white-egg hybrid data reviewed by Lewis (1987) and the findings of Etches (1990). An unpublished review of oviposition-time data for ISA Brown hens involved in experiments conducted at Bristol University between 1984 and 1998 (P.D. Lewis, personal communication) showed that egg-laying advanced by about 10 min per generation for a given photoperiod (Figure 3.3). The rates of advance in egg-laying time for hens on 8- and 16-h photoperiods were not significantly different, and the mean slope was described by the equation:

$$y = 335.3 - 0.170x + 0.394p \ (P=0.0004, r^2 = 0.972, \text{Slope SE} = 0.0237)$$

where y = mean oviposition time relative to dawn (h), x = year of the experiment, and p = photoperiod (h).

This earlier egg-laying is a likely consequence of the intense selection for increased egg production in modern hybrids and the associated reduction in egg-formation time (Gow *et al.*, 1984). This suggests that the later time of egg-laying by broiler breeders, compared with modern egg-type hybrids, is probably the result of the relatively relaxed selection pressure for egg numbers in broiler breeding programmes during that period, relative to egg-type hybrids, and not a difference in the location of the open period for preovulatory LH release.

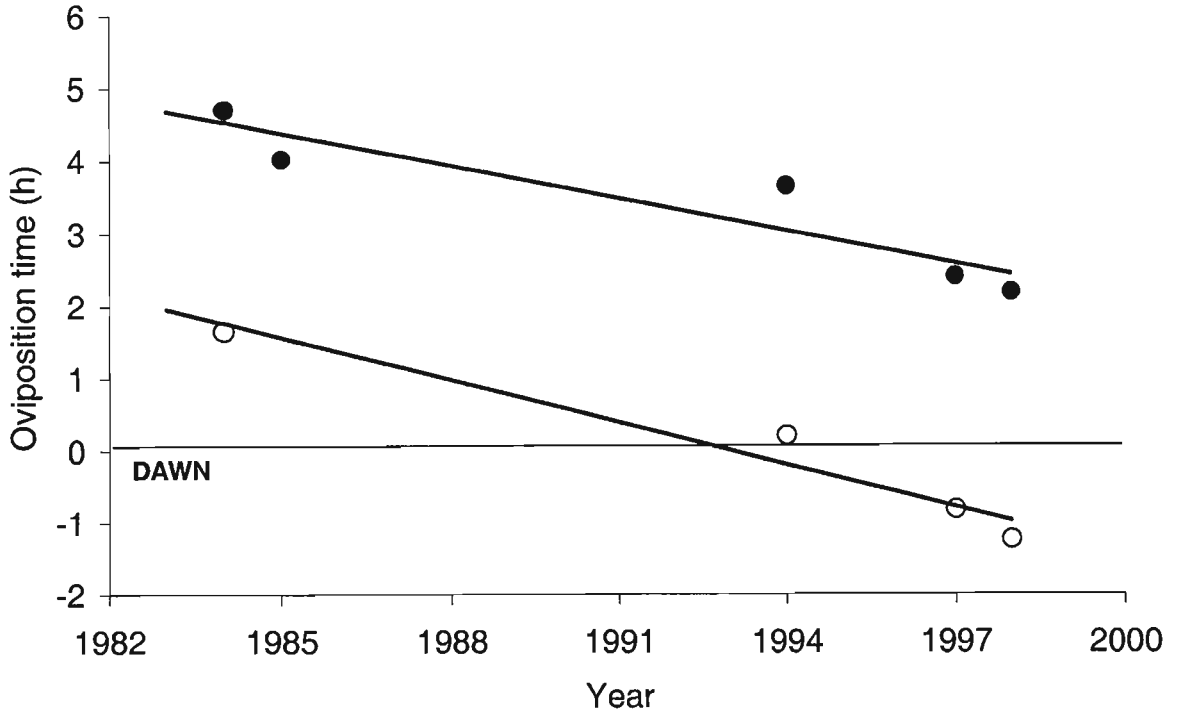

Figure 3.3. *Mean oviposition time (relative to dawn) for ISA Brown hybrids given an 8-h* (○) *or 16-h* (●) *photoperiod. Data from various experiments conducted between 1984 and 1998 at University of Bristol, UK (P.D. Lewis, personal communication).*

Results from this experiment and from a previous study (Etches, 1990) have shown that there is no further delay in egg-laying at photoperiods beyond a maximum in both broiler breeders and egg-type hens. However, this maximum photoperiod is different for the two types of fowl, being 14 h in broiler breeders (as determined in the current study) and 18 h in egg-type hens (Etches, 1990). Differences in egg formation time for meat-type and egg-type fowl might account for this disparity. Ovulation does not occur until about 30 to 45 min after the preceding oviposition (Etches, 1996a). A possible scenario could be that broiler breeders need a longer time for egg formation, and that the extra time spent in the oviduct by the potentially penultimate egg of a sequence prevents the potentially ultimate egg from being ovulated because the open period has been reached before the endocrine cascade of events has been initiated. Thus the earlier-laid, potentially penultimate egg becomes the ultimate in the sequence, the period of egg laying is curtailed, and mean oviposition is similar for 14 and 16-h

photoperiods despite a 1-h delay in oviposition time for the eggs laid earlier in the sequence. The termination of the open period under long daylengths (or short nights) is associated with low concentrations of plasma melatonin at the beginning of the photoperiod and an absence of an increase in plasma progesterone and, in turn, pre-ovulatory LH release and no ovulation (Nøddegaard, 1996). The 0.5 h/h continued advance in the time that half the day's eggs are laid, relative to the initiating dusk, confirms that it is an earlier cessation of egg laying for long photoperiods, rather than the lack of a shift in the phase setting of the open period, that is the most likely reason for the mean oviposition time for the 14- and 16-h photoperiods being similar.

CHAPTER 4

THE EFFECT OF PHOTOPERIOD ON BROILER BREEDER EGGSHELL QUALITY

4.1 INTRODUCTION

Both shell weight and shell thickness index for *ad libitum* fed commercial egg layers have been reported to decrease with photoperiod (Lewis *et al.*, 1994). However, increased rate of egg production, heavier egg weight, and higher feed intake, which generally result from exposing egg-type hybrids to longer photoperiods, have been discounted as reasons for the variations in shell quality (Lewis *et al.*, 1994). Instead, differences in the temporal relationship that shell formation has with feeding patterns, plasma calcium concentrations and the hormonal events that control the ovulatory cycle have been suggested as possible causal factors (Lewis *et al.*, 1994). Differences in the pattern of diurnal plasma melatonin concentration under the various photoperiods might also modify osteoblast and osteoclast activity (Cardinali *et* al., 2003), thereby influencing the mobilisation of calcium from medullary bone. However, this is conjectural because the molecular mechanisms that support the complicated movements of calcium during the shelling process are still poorly understood (Etches, 1996b).

The effect of photoperiod on shell quality is of practical importance because reduced shell quality can adversely affect fecundity, with poorer (thinner) shells being associated with increased weight loss during incubation (McDaniel *et al.*, 1979), and reduced hatchability, and increased embryonic mortality for eggs with a specific gravity <1.080 (McDaniel *et al.*, 1981; Roque and Soares, 1994).

Photoperiodic influences on shell quality in broiler breeders has not been reported, and so a study was made to determine shell weight and shell thickness index data for 52-week old broiler breeders maintained on six different photoperiods from 3 d of age.

4.2 MATERIALS AND METHODS

Eggs were collected for shell quality determination using the birds in Experiment 1 according to two protocols: (1) on 1 d at 52 weeks, after an initial egg collection at 07.30, the next 10 eggs to be laid in each of the 32 pens, and (2) on 1 d at 53 weeks, hourly from the first egg onwards, from the 8 pens in the two rooms given 13 or 14-h photoperiods. This second exercise was conducted to assess any effect on shell quality of eggs being laid at different times relative to both dawn and start of egg-laying (and so later in the sequence) by the groups on the various photoperiods. This information would then give a measure of the contribution that the changes in egg-laying time effected by the different photoperiods (as reported in Chapter 3) might have made towards shell quality when, in the first exercise, eggs were collected at the same time of the day. Eggs were individually weighed to 0.1 g, the contents removed and shells dried to constant weight loss (4 to 5 h at 100°C). Eggshells were then weighed (EW, mg), the surface area of the egg (S, cm^2) estimated using the equation $S = 3.9782EW^{0.7056}$ (Nordstrom and Ousterhout, 1982), and the shell thickness index (mg/cm^2) calculated.

The shell quality means were regressed on photoperiod using a model from Genstat 6th Edition (Lawes Agricultural Trust, 2002).

4.3 RESULTS AND DISCUSSION

Mean egg weight, shell weight and shell thickness index for the various photoperiods are given in Table 4.1 (protocol 1) and Table 4.2 (protocol 2).

Table 4.1. *Mean egg weight, shell weight and shell thickness index for broiler breeder hens given various photoperiods (protocol 1).*

Photoperiod	Egg weight (g)	Shell weight (mg)	Shell thickness index (mg/cm^2)
10	74.4 ± 5.54	6840 ± 741.0	82.29 ± 7.178
11	73.2 ± 4.66	6702 ± 656.8	81.48 ± 6.200
12	74.3 ± 4.75	6891 ± 691.2	82.94 ± 6.532
13	75.0 ± 4.17	6839 ± 593.3	81.87 ± 5.596
14	75.1 ± 4.83	6693 ± 577.3	80.07 ± 5.797
16	75.6 ± 5.14	6634 ± 619.3	79.02 ± 6.374

Table 4.2. *Mean egg weight, shell weight and shell thickness index of eggs laid at different times for broiler breeder hens given 13- or 14-h photoperiods (protocol 2).*

Photoperiod	Time (h after first egg)	Egg weight (g)	Shell weight (mg)	Shell thickness index (mg/cm^2)
13	1	72.6 ± 5.18	6413 ± 688.9	78.34 ± 5.272
	2	76.5 ± 4.33	6978 ± 635.3	82.14 ± 5.734
	3	74.0 ± 4.77	6794 ± 600.8	81.96 ± 5.421
	4	74.0 ± 5.37	6762 ± 575.9	81.60 ± 5.757
	5	73.1 ± 4.93	6854 ± 588.5	83.32 ± 4.744
	6	71.0 ± 4.99	6356 ± 766.3	78.94 ± 8.245
	7	72.8 ± 5.56	6756 ± 731.1	82.31 ± 5.820
	8	73.4 ± 3.83	7012 ± 568.0	85.04 ± 5.715
	9	73.1 ± 4.67	6705 ± 311.4	81.72 ± 4.141
	10	71.8 ± 7.71	6829 ± 789.5	84.10 ± 5.564
14	1	76.0 ± 3.43	6628 ± 431.2	78.49 ± 4.938
	2	76.4 ± 5.77	7017 ± 694.5	82.68 ± 5.370
	3	75.7 ± 5.48	6716 ± 788.7	79.64 ± 7.493
	4	74.2 ± 4.92	6628 ± 790.0	79.78 ± 8.146
	5	74.2 ± 4.76	6683 ± 440.8	80.61 ± 5.670
	6	75.4 ± 4.45	6821 ± 550.5	81.18 ± 4.980
	7	74.1 ± 7.30	6543 ± 331.1	79.08 ± 3.387
	8	74.5 ± 3.99	6935 ± 637.7	83.20 ± 5.756
	9	75.6 ± 4.30	6977 ± 487.5	82.90 ± 4.556
	10	74.0 ± 4.22	6638 ± 589.9	80.16 ± 7.324

Egg weight increased by 0.31 g for each 1-h increase in photoperiod (r^2 = 0.635, slope SE = 0.117, P=0.058). Whilst this is slightly higher than the 0.25 g/h observed for egg-type hybrids for the laying year (P.D. Lewis, *unpublished data*), broiler breeder eggs at 52 weeks are heavier than the mean weight for a laying cycle in egg-type birds, and, in both cases, the hourly increase represented a 0.4% increase in egg weight. As shown in Figure 4.1, shell weight tended to decrease with photoperiod by about 30 mg/h (P=0.194), and, although this trend is not statistically significant, it is still in the same direction as the -61 mg/h change reported by Lewis *et al.* (1994) for ISA Brown egg-type hybrids. A combination of the increasing egg weight and decreasing shell weight resulted in a significant decrease in shell thickness index of 0.57 mg/cm² for each 1-h extension of the photoperiod (r^2 = 0.696, slope SE = 0.189, P=0.039). This compares with -0.48 mg/cm² per hour for ISA Brown hybrids (Lewis *et al.*, 1994). Whilst there were significant differences in rate of lay between photoperiods, no significant relationship was found between shell thickness index and rate of lay at 52 weeks.

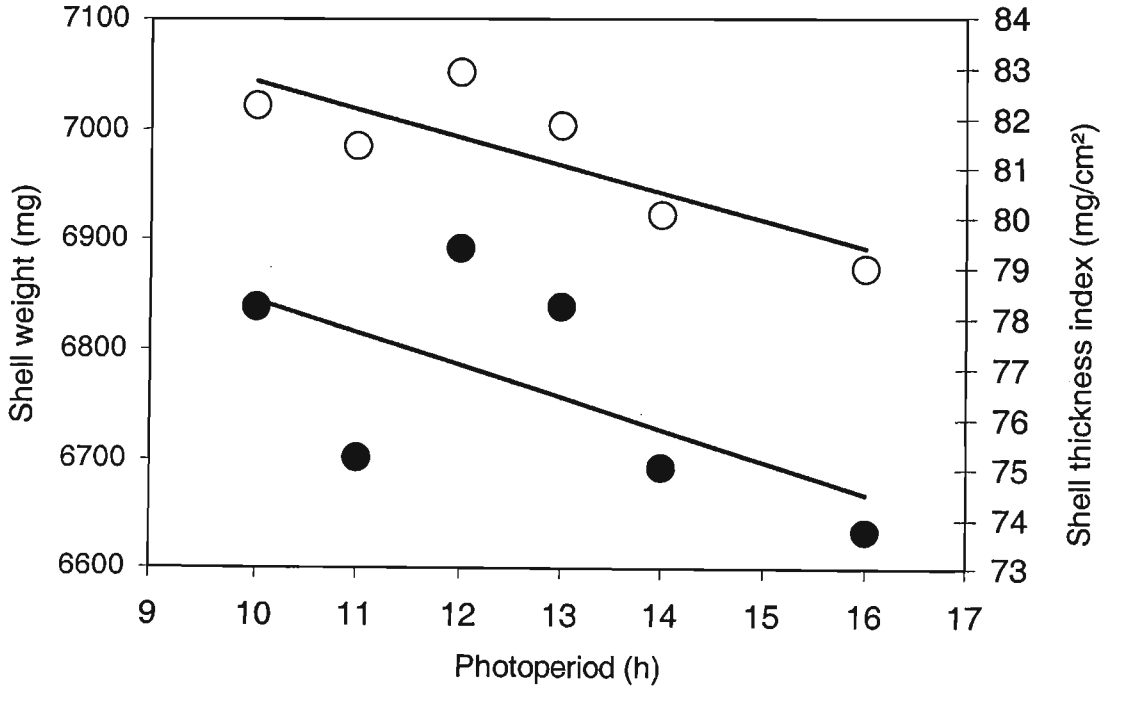

Figure 4.1. Regressions of shell weight (•, mg) and shell thickness index (○, mg/cm²) on photoperiod (h) for Cobb 500 broiler breeders at 52 weeks of age.

Under the second egg collection protocol, the effect of time of lay on egg weight, shell weight and shell thickness index was investigated. Eggs laid in the first hour from the start of that day's egg-laying were omitted from all regressions, because these would have included the first eggs of sequences which typically are abnormally larger and have disproportionately poorer shells than eggs of the remainder of the sequence (Belyavin *et al.*, 1987). Additionally, data for the two photoperiod groups (13- and 14-h) were pooled, since there were no significant differences in the slope of the response of any of the variables (egg weight, shell weight and shell thickness index) to time of lay.

Mean egg weight for the two photoperiod groups decreased significantly by 0.27 g/h (r^2 = 0.543, slope SE = 0.096, P= 0.013) from the second hour of lay onwards, although eggs from birds on 14-h photoperiods had a mean weight that was 1.55 g significantly heavier than 13-h. Shell weight was unaffected by the time of lay (P=0.942), with no differences between the 13- and 14-h groups. Eggshell thickness index increased marginally through the day by 0.16 mg/cm^2 per hour (P=0.315) and eggs laid by hens on 14-h photoperiods tended to have thinner shell thicknesses than the 13-h (P=0.131) ones. Though not statistically significant, these differences are in the directions to be expected for later egg-laying (Belyavin *et al.*, 1987) and longer photoperiods (Lewis *et al.*, 1994).

It can be concluded that hens given longer photoperiods do lay eggs that have shells that are lower in weight and have a lower shell thickness index than those on shorter photoperiods. Whilst shell weight did not change with time of lay within the day, it did decrease as daylength was increased, in the manner reported for egg-type hybrids where all eggs had been measured (Lewis *et al.*, 1994). The significant deterioration in shell thickness index with increasing daylength (0.57 mg/cm^2 per hour of photoperiod) exceeded the non-significant 0.16 mg/cm^2 per hour of egg-laying time improvement for eggs laid later in the day. Collecting eggs at the same chronological time in the first exercise would have resulted in eggs laid by hens on the shorter photoperiods being from a later part of the sequence, and so likely to have been of better quality, than those laid earlier in the sequence by birds on longer photoperiods. As determined in Chapter 3, oviposition time for broiler breeders is delayed relative to dawn by about 30 min for each 1-h extension of the photoperiod, and, as a consequence, the

improvement in shell thickness index to be predicted for the eggs on the shorter photoperiods would only be half the 0.16 mg/cm^2 per hour improvement attributed to later egg-laying within the day. Therefore, a 0.49 mg/cm^2 per hour difference in quality deterioration (0.57-0.08) could be concluded to be the photoperiodic influence. This concurs remarkably well with the 0.48 mg/cm^2 per hour observed in egg-type hybrids, where time of lay had no influence because all eggs laid in the day were measured (Lewis *et al.*, 1994). Because shell quality and hatchability are closely correlated (McDaniel *et al.*, 1981; Roque and Soares, 1994), these findings suggest that the hatchability of eggs laid by hens on long photoperiods, especially those produced later in the laying year, might well be inferior to that for birds maintained on shorter photoperiods. Therefore, the effect of photoperiod on hatchability may be worthy of further investigation.

CHAPTER 5

THE EFFECT OF FEEDING TIME ON BROILER BREEDER EGGSHELL QUALITY AND OVIPOSITION TIME

5.1 INTRODUCTION

Broiler breeders are usually provided a limited daily allowance of feed in the morning. This practice does not supply nutrients to coincide with the hen's need, particularly for shell formation (Bootwalla *et al.*, 1983), which normally commences in the afternoon or evening. This is due to broiler breeders being unable to meter calcium (Ca) from the crop to the lower digestive tract at a uniform rate (Farmer *et al.*, 1983a). It may be possible to improve eggshell quality if nutrients are supplied at times that correspond more closely to periods of shell deposition by changing the time of feed intake. Bootwalla *et al.* (1983), Farmer *et al.* (1983c), Brake (1988) and Harms (1991) reported increases in egg specific gravity when birds were fed later in the day. Lewis and Perry (1988) reported an increase in shell thickness and shell weight when broiler breeders were fed half the daily food allocation twice daily compared to a single allocation of food provided in the morning. However, experiments performed by Brake (1985), Wilson and Keeling (1991), and Samara *et al.* (1996) showed no effect of feeding time on eggshell quality.

Although afternoon feeding of broiler breeders may improve shell quality, there is a potential concern, substantiated by subjective commercial observations (Lewis and Perry, 1988), that delaying feeding may delay oviposition. Such delays may cause egg collection problems in that a large proportion of eggs may be laid late in the afternoon or in the early evening, after the final egg collection of the day. Various researchers have attempted to determine whether changing the time of feeding alters oviposition time, with contradictory conclusions. Harms (1991) and Samara *et al.* (1996) reported a delay in the time of oviposition when broiler breeders were fed later in the day. A similar response was observed in cross-bred layers (Daniel and Balnave, 1981) and Japanese quail (Hassan *et al.*, 2003). However, no difference in oviposition times was observed between morning- and afternoon-fed breeders (Brake,1985)

or between broiler breeders fed a single allocation of food in the morning or half the daily food allocation twice a day (Lewis and Perry, 1988). On the contrary, Wilson and Keeling (1991) reported a delay in oviposition time due to afternoon feeding in standard sized broiler breeders, but observed no such response in dwarf breeders.

Due to contradictions in the literature, three experiments were performed to determine the effect of feeding time on shell quality and oviposition time in broiler breeders.

5.2 MATERIALS AND METHODS

In Experiment 3, 432 24-week old 'Cobb 500' broiler breeder females from an earlier trial were housed in individual cages in a closed house and subjected to a 14-h artificial photoperiod from 07.00 to 21.00. Six feeding treatments, each replicated twice, were applied to 32 weeks of age. The feeding treatments were different times at which birds were fed a daily allocation of 165 g of a commercial broiler breeder layer feed (139 g CP/kg, 12.2 MJ TMEn/kg, 33 g Ca/kg). The feeding times were 07.30, 09.30, 11.30, 13.30 or 15.30; and one treatment in which birds were fed half the daily feed allocation at 07.30 and half at 15.30 (half-feeding). The numbers of normal, soft-shelled, cracked and double-yolked eggs produced were recorded daily. Eggs were collected at half-hourly intervals between 06.00 and 21.00 during two 2-d periods, at 28 and 31 weeks. Egg weight and shell thickness data were determined from randomly selected normal eggs using 80 eggs per treatment at 28 weeks, and 40 eggs per treatment at 31 and 32 weeks.

In Experiment 4, 800 57-week old 'Cobb 500' broiler breeder females were housed on litter floor pens (50 per pen) in a curtain-sided house and subjected to a 14-h photoperiod from 05.00 to 19.00. The birds were given a single daily feed allocation of 150 g of a commercial broiler breeder layer feed (145 g CP/kg, 11.5 MJ TMEn/kg, 35 g Ca/kg) at 07.30, 10.00, 13.00 or 15.30, each represented in 4 pens. Eggs were collected hourly from 04.00 to 19.00 during two 2-d periods, at 58 and 59 weeks. Egg weight and shell thickness were measured for all normal eggs laid on 1 d at 59 weeks of age.

In Experiment 5, 240 35-week old 'Cobb 500' broiler breeder females were housed in 60 individual cages in each of 4 light-tight rooms and subjected to a 16-h photoperiod from 07.00 to 23.00. Within each room, 15 birds were given 170 g of a commercial broiler breeder layer feed (150 g CP/kg, 11.6 MJ TMEn/kg, 26 g Ca/kg) daily at 07.30, 10.00, 13.00 or 15.30. Oviposition times were monitored from 06.00 to 21.00 during three 2-d periods between 36 and 37 weeks. For each feeding time, and for each 1-h period between 10.00 and 16.00, egg weight and shell thickness measurements were taken from five randomly selected normal eggs, pooled from all four rooms.

In all cases, shell thickness was measured with a micrometer* at two points on the equator of each egg. Egg production data from Experiment 3 were subjected to analysis of variance. In all three experiments, the effects of feeding time on egg weight, shell thickness and oviposition time were analysed using linear regression. Statistical analyses were performed using Genstat 6th edition (Lawes Agricultural Trust, 2002).

5.3 RESULTS AND DISCUSSION

Feeding time had no significant effect on total, broken and soft-shelled or double-yolked egg production from 26 to 32 weeks in Experiment 3. Mean egg weight and shell thickness for the various feeding times in Experiments 3, 4 and 5 are shown in Table 5.1. A regression was performed on shell thickness data from Experiments 3 and 5 with differences between trial means removed by fitting a constant to data from Experiment 5 by least squares. The equation describing the regression was:

$$y = 380 + 3.5F \qquad (P<0.001, r^2 = 0.998, \text{Slope SE} = 0.17)$$

where y = shell thickness (μm) and F = feeding time (h after lights on), as shown in Figure 5.1. In Experiment 3, the half-feeding treatment resulted in a mean shell thickness of 397 ± 34.6 μm which, according to the regression equation, corresponds to a single feeding at approximately 4.9 h after lights on. In Experiment 4, no significant response of eggshell thickness to feeding time was observed (Figure 5.1). Egg weight was not significantly affected by feeding time in all three experiments.

* Mitutoyo model no. 103-129, Mitutoyo UK Ltd, West Point Business Park, Andover, Hampshire, SP 10 3UX

Table 5.1. *Mean egg weight and shell thickness for broiler breeder hens fed at different times in Experiments 3, 4 and 5.*

Feeding time	Egg weight (g)	Shell thickness (μm)
Experiment 3		
07.30	61.8 ± 3.70	382 ± 30.3
09.30	62.0 ± 4.65	389 ± 31.1
11.30	61.3 ± 4.18	396 ± 32.7
13.30	62.1 ± 4.58	404 ± 34.7
15.30	61.9 ± 4.27	409 ± 29.6
Half-feeding	62.0 ± 3.79	397 ± 34.6
Experiment 4		
07.30	72.4 ± 6.97	392 ± 31.6
10.00	73.5 ± 4.67	398 ± 33.1
13.00	75.5 ± 4.32	398 ± 27.8
15.30	75.2 ± 5.01	395 ± 36.2
Experiment 5		
07.30	66.5 ± 3.57	323 ± 21.9 (381) [1]
10.00	65.7 ± 2.83	335 ± 23.1 (393) [1]
13.00	64.3 ± 4.58	342 ± 29.1 (399) [1]
15.30	66.6 ± 4.02	354 ± 27.3 (412) [1]

[1] Means adjusted by least squares for differences from Experiment 3 in parentheses.

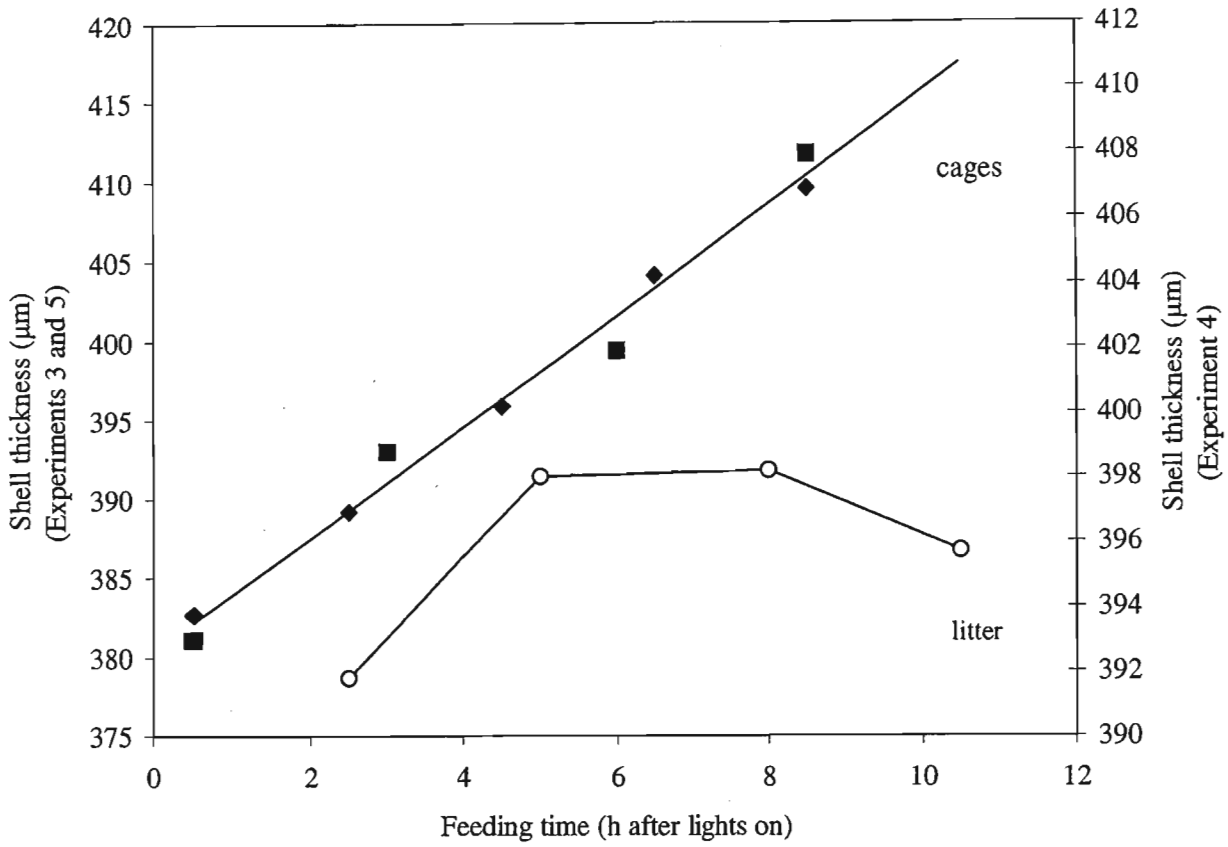

Figure 5.1. *The effect of delaying feeding on shell thickness of Cobb 500 broiler breeders housed in individual cages or in litter pens (♦ Experiment 3, ○ Experiment 4, ■ adjusted Experiment 5).*

The observed increase in eggshell thickness due to delayed feeding in Experiments 3 and 5 is in agreement with other studies (Bootwalla *et al.*, 1983; Farmer *et al.*, 1983c; Brake 1988; Harms, 1991). The lack of a significant difference in egg weight suggests that the improvement in shell thickness was not due to increased egg formation time but rather to improved calcium utilisation, as explained by Farmer *et al.* (1983c) and Roland and Farmer (1984). In morning fed birds, a large proportion of ingested Ca passes through the digestive tract before the initiation of shell calcification (Farmer *et al.*, 1983c). Consequently, these hens have to store most of the Ca in the bone and, therefore, the route Ca takes to the eggshell for morning-fed birds is via the small intestine to blood to bone to shell gland and eventually to shell. However, when feeding is delayed, the period of shell deposition is closer to the time of feeding which results in afternoon-fed birds having a greater proportion of retained Ca in

the gastrointestinal tract at the commencement of shell formation than morning-fed birds (Farmer *et al.*, 1983a). A negative correlation exists between bone mobilisation and eggshell weight (Sauveur and Mongin, 1983b) and quality (Farmer *et al.*, 1986). Thus, delayed feeding improves shell thickness by allowing more Ca to bypass the bone and be deposited directly on the egg via the blood (Roland and Farmer, 1984).

The lack of response in shell thickness to feeding time in Experiment 4 is in contrast with the findings of Experiments 3 and 5, but in agreement with the results of Brake (1985) and Wilson and Keeling (1991). Differences between results of the three trials may be due to housing system. Harms *et al.* (1984) reported that the specific gravity of eggs from broiler breeder hens maintained on litter is significantly higher than that from hens maintained on wire. However, when the hens on wire had access to litter from floor pens, the specific gravity of eggs was equal to that from hens on litter; this improvement in egg specific gravity probably being due to the intake of Ca contained in the litter. Therefore, the lack of an effect of feeding time on shell thickness in Experiment 4, where hens were housed on litter floors, and in the experiments performed by Brake (1985) and Wilson and Keeling (1991), where birds were housed on litter and slats, may be due to recycling of nutrients, such as Ca, in the litter (Bootwalla *et al.*, 1983; Harms, 1991). Other factors may also play a role, such as competition for feed resulting in hens on the same treatment having unequal feed intakes. However, in spite of such factors, a number of floor-pen studies have yielded significant increases in eggshell quality due to delayed feeding times (Bootwalla *et al.*, 1983; Farmer *et al.*, 1983c; Brake, 1988; Harms, 1991).

Mean oviposition time (relative to dawn) for the various feeding times in Experiments 3, 4 and 5 are given in Table 5.2. A regression using data from all three experiments was performed to determine the response of mean oviposition time (MOT) to feeding time. Differences between trial means were removed by fitting constants to data from Experiments 3 and 4 by least squares. The equation describing the regression was:

$$y = 5.762 + 0.0807F \qquad (P<0.01, r^2 = 0.687, \text{Slope SE} = 0.0184)$$

where y = MOT (h after lights on) and F = feeding time (h after lights on). It is important to consider the close proximity of the hens on the various treatments in all experiments.

Oviposition times of later-fed birds may have been synchronised to some extent by stress resulting from the feeding of birds on earlier feeding treatments. The delay in MOT by 4.8 ± 1.10 min per h delay in feeding time (Figure 5.2) may thus be an underestimate of the effect of feeding time on oviposition time. Delays in oviposition times may be greater than indicated in the current study when delayed feeding is employed in entirely separate houses. The lack of a significant difference in egg weight rules out the possibility that increased transit times through the oviduct may account for such differences in oviposition time and suggests that feeding time has some influence on the timing of the open period for LH release.

Table 5.2. *Mean oviposition time (h.min) relative to the start of the photoperiod in which the oviposition occurred for broiler breeder hens fed at different times in Experiments 3, 4 and 5.*

Feeding time	Mean oviposition time
Experiment 3	
07.30	5.44 ± 0.16 (6.04) [1]
09.30	5.39 ± 0.13 (5.59) [1]
11.30	5.33 ± 0.12 (5.53) [1]
13.30	5.39 ± 0.15 (5.59) [1]
15.30	6.22 ± 0.08 (6.42) [1]
Half-feeding	5.11 ± 0.12 (5.31) [1]
Experiment 4	
07.30	5.39 ± 0.05 (5.47) [1]
10.00	6.07 ± 0.02 (6.14) [1]
13.00	6.18 ± 0.05 (6.26) [1]
15.30	6.34 ± 0.12 (6.41) [1]
Experiment 5	
07.30	5.49 ± 0.10
10.00	6.04 ± 0.03
13.00	6.11 ± 0.14
15.30	6.26 ± 0.11

[1] Means adjusted by least squares for differences from Experiment 5 in parentheses.

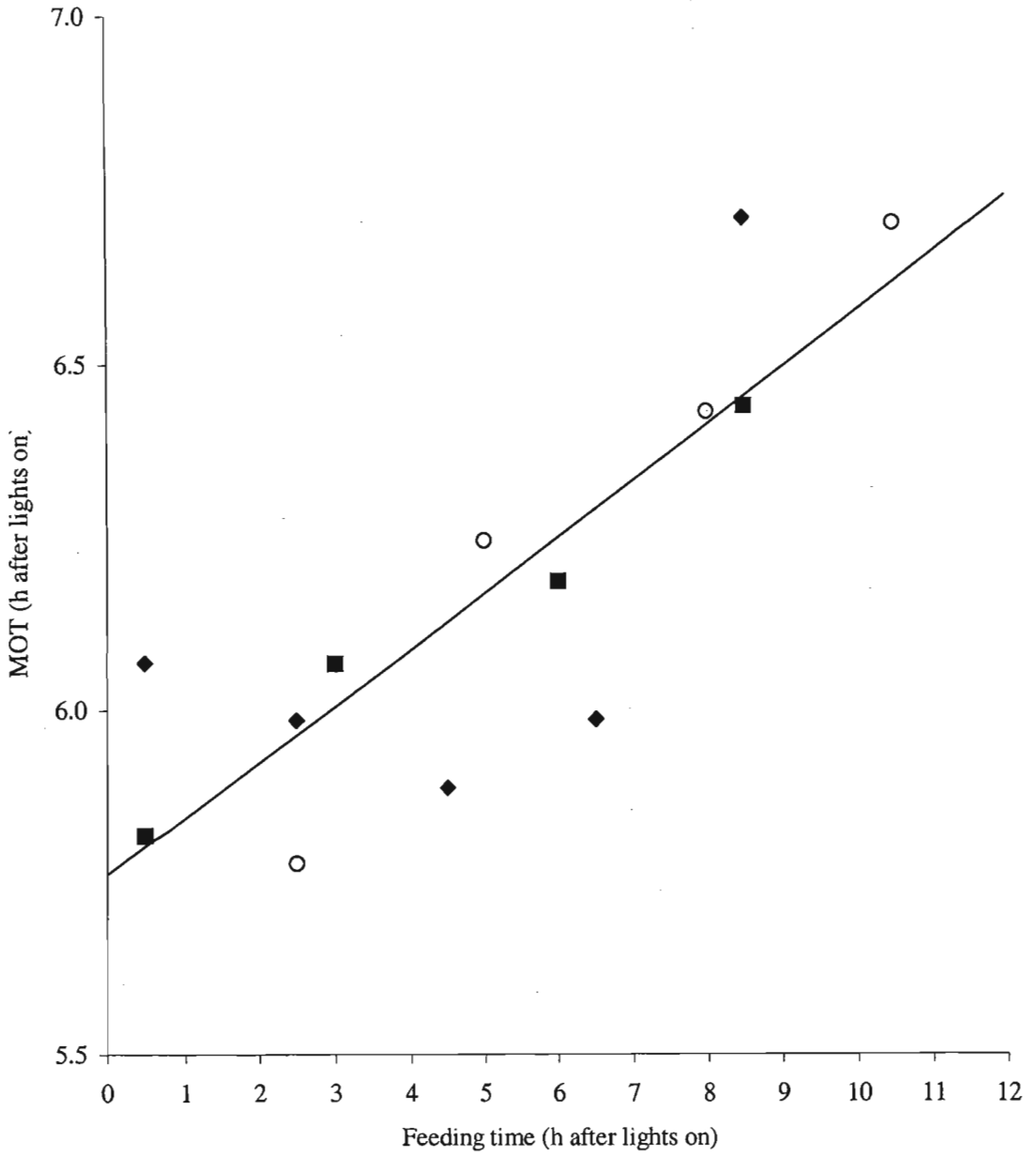

Figure 5.2. *Mean oviposition time (MOT) for Cobb 500 broiler breeders fed at various times relative to lights on (♦ adjusted Experiment 3, ○ adjusted Experiment 4, ■ Experiment 5).*

The results of these experiments suggest that the time of day when broiler breeders are fed influences shell thickness by altering the amount of readily available Ca in the digestive tract during shell calcification. Delaying feeding improves shell quality, although improvements

may only be marginal in flocks that are housed on the floor. Delaying feeding results in delayed oviposition times, which may have unwanted consequences, such as eggs being laid later in the day. In order to prevent such problems, producers who wish to implement delayed feeding could turn lights on earlier in the morning to ensure that most eggs are laid before the final egg collection of the day.

CHAPTER 6

CONCLUSIONS

The work presented in this thesis has shown that hens given longer photoperiods lay eggs that have poorer shell quality than those on shorter photoperiods. The validity of current commercial practices in which broiler breeder flocks are subject to photoperiods that are in excess of the photoperiod required for maximum egg production should thus be questioned. Apart from being unnecessary and costly, providing broiler breeders with excessively long photoperiods may be a cause of depressed eggshell thickness with consequential low hatchability.

In order to improve eggshell quality, broiler breeders could be subjected to shorter photoperiods, provided that the photoperiod is not shorter than that necessary for maximum egg production. However, as is evident in the current study, the length of the photoperiod alters oviposition time, with birds on shorter photoperiods laying eggs earlier in the subjective day than birds on longer photoperiods. Producers should thus ensure that the photoperiod is not so short as to increase the proportion of eggs laid before dawn, as these eggs, being laid in the dark, would most likely be floor eggs that are unsuitable for incubation.

The current study has shown that eggshell quality can be improved by delaying the time of feeding, although improvements may only be marginal in broiler breeder flocks that are housed on litter floors. However, delaying the time of feeding may cause a delay in oviposition times. Producers who wish to implement delayed feeding should thus consider the management implications of eggs being laid later in the day.

The results of the current study have raised interesting and pertinent issues that need to be addressed.

Hatchability was not measured in this study, and therefore any adverse effect of long photoperiods, and any advantages of delayed feeding, on hatchability can only be inferred.

More research is required to determine the effect of photoperiod and feeding time on hatchability in particular.

It is still unknown why eggshell thickness of laying-type hybrids and broiler breeders is negatively correlated with photoperiod. Differences in the temporal relationship that the shelling process has with feeding (and plasma calcium concentrations) patterns, and the hormonal events that control the ovulatory cycle have been suggested as causal factors. More research is needed to improve our understanding of the molecular mechanisms that support the complicated movements of calcium during the shelling process in order to find the reasons for the adverse effect of long photoperiods on eggshell quality.

Eggshell quality is an important factor to consider in broiler breeder production. In order to produce the maximum number of broiler chicks, producers must not only maximize egg production, but also ensure that eggshell quality is of a standard that will promote hatchability. It is hoped that the application of the results reported in the current study and further experimentation in this field will provide a means by which this can be accomplished.

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