PHOTIC INVOLVEMENT IN THE REPRODUCTIVE PHYSIOLOGY OF FEMALE DOMESTIC FOWL

by

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This thesis is dedicated to my wife, Jean, for tolerating our periods of separation and keeping home going whilst I have been studying the photoperiodic response of broiler breeders in South Africa, and to the late Graham Perry, without whose encouragement I would never have entered the world of poultry lighting research in the first place.

Thanks are also due to Trevor Morris for the many hours spent discussing diverse aspects of poultry lighting over the past 20 years, and to Rob Gous for his support of the broiler breeder research conducted at the University of KwaZulu-Natal since 2000.

As the candidate's Supervisor I agree to submission of this thesis.

Professor Rob M. Gous

DECLARATION

I **Peter David Lewis** declare that:

(i)   The research reported in this thesis, except where otherwise indicated, is my original research.

(ii)   This thesis has not been submitted for any degree or examination at any other university.

(iii)   This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from those persons.

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Signed: …………………………………… Date …………………………………

FREQUENTLY USED ABBREVIATIONS

AFE = age at first egg

ASM = age at sexual maturity ($\approx$ 50% egg production)

FSH = Follicle Stimulating Hormone

LH = Luteinizing Hormone

MOT = mean oviposition time

PIP = photoinducible phase

SD = standard deviation

SEM = standard error of the mean

UV-A = ultraviolet radiation between 320 and 400 nm

SYNONYMS

Dawn, sunrise, start of photoperiod, dark-light interface

Dusk, sunset, end of photoperiod, light-dark interface

Intermittent lighting, interrupted lighting

Light intensity, illuminance

Long day, stimulatory photoperiod

Photoperiod, period of light, daylength, day

Scotoperiod, period of darkness, night

Short day, non-stimulatory photoperiod

LIGHTING REGIMEN DESCRIPTIONS

D = dark period

L = light period

Conventional regimen: e.g., 8L:16D = 8 h light, 16 h darkness

Symmetrical interrupted regimen: e.g., 4(3.5L:2.5D) = repeating cycles of 3.5 h light and
    2.5 h darkness

Asymmetrical interrupted regimen: e.g., 8L:4D:2L:10D = 8 h light, 4 h darkness, 2 h light,
    10 h darkness

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A1. Poultry lighting research pre-1983

There has been an awareness for at least four centuries that lighting can influence avian reproductive physiology; Dutch bird-netters in the seventeenth century kept captive wild birds on short days during spring and summer months to delay vernal bird song, and then transferred them to long days at the end of summer so that they could be used as decoys to facilitate the netting of autumn migrants (Hoos, 1937). However, the first demonstration of the effects of artificial lighting on the reproductive performance of domestic fowl was almost certainly a series of three experiments conducted between 1889 and 1893 in America (Waldorf, 1920). Dr Waldorf, a general practitioner in Buffalo, New York State, observed improvements in egg production, fertility, and hatchability in domestic hens that had been given constant a 16.5-h photoperiod from gas-burning lanterns during the short days of winter. The use of artificial lighting during winter to improve egg production appears to have been used practically from very early in the 20th century. In 1907, Prof. Halpin of the Wisconsin College of Agriculture related that a farmer in Michigan had been using the technique for several years. The farmer had discovered the benefits by accident when he noticed that the hens in the pen next to his horses, which were fed daily at 5.00 am, laid more eggs than hens in the other pens (Curtis, 1920). The first formal research into lighting for laying hens was conducted by George Shoup at the Washington State College of Agriculture, Puyallup between 1912 and 1917 (Shoup, 1920). Subsequently, many American agricultural experiment stations contributed to our knowledge of supplemental lighting (e.g., Ogle and Lamoreux, 1942; Callenbach *et al*., 1943; Byerly and Knox, 1946; Dobie *et al*., 1946).

Photoperiod: Observations of seasonal variation in sexual maturation and egg production (Whetham, 1933; Hutchinson and Taylor, 1957; Morris and Fox, 1958*a*; Kinder and Funk, 1960) prompted studies of the effects of changing photoperiod, and the findings

still form the basis of most of the commercial lighting programmes in use today (e.g., Sykes, 1956; Marr *et al*., 1962; Hutchinson and Taylor, 1957; Morris and Fox, 1958*b*, 1960, 1961, King, 1959, 1961; Bowman, 1960; Bowman and Jones, 1961, 1963, 1964, 1966; Smith and Noles, 1963; Morris, 1962, 1967*a*; Morris *et al*., 1964; Lillie and Denton, 1965). Much of this work was conducted by Trevor Morris and co-workers at the University of Reading.

Illuminance: The first studies of the effect of light intensity on reproductive performance were conducted in America (Nicholas *et al*., 1944; Dobie *et al*., 1946; Ostrander *et al*., 1960), but the general response of growing pullets and laying hens to illuminance was subsequently defined at the University of Reading by Morris and Owen (1966) and Morris (1967*b*).

Ultraviolet radiation: There have been several reports of the effect of UV-A radiation on the prevention of vitamin D_3 deficiency (e.g., Mussehl and Ackerson, 1931), ocular integrity (Barnett and Laursen-Jones, 1976), egg production (e.g., Titus and Nestler, 1935), and shell quality (e.g., Hart *et al*., 1925) in domestic fowl, but there was none for the effect of UV-A on the photosexual response.

Interrupted lighting: Originally, the asymmetrical form of interrupted lighting (regimens that have more than one period of light and darkness each 24 h) was used by physiologists to investigate various aspects of the avian photoperiodic response; for example, the minimum amount of illumination required to support satisfactory levels of egg production (e.g., Dobie *et al*., 1946; Wilson and Abplanalp, 1956) and the photo-inducible phase (van Tienhoven and Ostrander, 1973). Subsequently, rising energy and feed prices triggered a renewal of interest in both asymmetrical and symmetrical regimens for their economic benefits to commercial egg production (e.g., Snetsinger *et al*., 1979; Nys and Mongin, 1981; Sauveur and Mongin, 1983; Lewis and Perry, 1990*a*,*b*; Morris *et al*., 1988, 1990; Morris and Butler, 1995).

A2. Poultry lighting research conducted by Peter Lewis since 1983

The commentary describes the principle findings from studies of the involvement of light in the photosexual responses of egg-type and broiler breeder female domestic fowl conducted at the Universities of Bristol (UK), Guelph (Canada), Natal, and KwaZulu-Natal (South Africa) since 1983. I conducted the early research as a Ph.D. student, but since 1987 my involvement with research has been as an Honorary Research Fellow (Bristol 1993-1995, Natal 2001-2003, KwaZulu-Natal 2003 to present), Honorary Senior Research Fellow (Reading 1996-2002), Visiting Fellow of Medicine (Bristol 2000-2003), and Adjunct Professor (Guelph 2003-2006).

The initial investigations, conducted within the School of Veterinary Science in the Faculty of Medicine at the University of Bristol, were of the responses of egg-laying hens to interrupted lighting regimens, and these led to the award of a Ph.D. degree by the University of Bristol in 1987. Subsequently, the focus of research at Bristol changed from interrupted lighting to the photic control of sexual maturation in egg-type pullets, culminating in the creation of predictive models for age at first egg in pullets maintained on constant photoperiods, and those given a single change or two opposing changes in photoperiod. Whilst at Bristol, studies were also made of the interacting role of dietary iodine in the ovulatory cycle (Lewis, 2004; Perry *et al*., 1989, 1990), correlations of water and fat contents in poultry carcasses and the creation of a model to predict fat content from dry matter (Lewis and Perry, 1987a, 1991a), infertility in laying hens (Long and Lewis, 1990; Lewis and Long, 1992), performance and sensory attributes of broiler and 'Label Rouge' genotypes and their production systems (Lewis *et al*., 1997*a*; Farmer *et al*., 1991, 1992, 1997), the role of lighting and UV-A radiation in the performance and behaviour of intact male turkeys (Lewis *et al*., 1998*b*,*c*, 2000c, Moinard *et al*., 2001, Sherwin *et al*.,

1999*a,b*) and laying hens (Lewis *et al*., 2000*a*), and the replacement of light with noise (Lewis and Perry, *VIII European Poultry Conference*, 1990); comments on these studies have not been included in this commentary.

The research in the Animal and Poultry Science Department at the University of Guelph centred on the role of photoperiod, illuminance, and light colour during the rearing period in the timing of sexual maturation and subsequent egg production in brown-egg and white-egg strains of laying hen.

Current work in the Discipline of Animal and Poultry Science at the University of KwaZulu-Natal, formerly University of Natal, has established that broiler breeders exhibit photorefractoriness and demonstrated the necessity for lighting regimens to be designed specifically for broiler breeders. The work has also shown the significant modifying effect of growth rate on the broiler breeder's photosexual response, and led to the creation of a model to predict age at sexual maturity from both lighting and body weight inputs.

Studies of some of the mechanisms involved in the photosexual response have also been conducted at the University of KwaZulu-Natal. These included a possible role for melatonin as a transmitter of photoperiodic information to the hypothalamus, responses of egg-type hybrids to temporary transfers to long days, and the potential to make short days mildly stimulatory by supplementing them with radio noise.

Key publications

- Conclusions that the effect of a constant photoperiod on age at first egg in egg-type pullets is better described by a hinge than by a curvilinear model, and that 10 h and not 16 to 17 h induces the earliest maturity (**Lewis *et al*., 1998*a***).
- Creation of a model to predict age at first in egg-type pullets given a single change in photoperiod (**Lewis *et al*., 2002**).

- An hypothesis that an initial change in photoperiod alters a pullet's physiological age so it responds to a subsequent opposing change in photoperiod, in terms of rate of sexual maturation, as if the change had been made at the bird's 'physiological age' and not at its chronological age (**Lewis *et al*., 2003*b***). This hypothesis is currently being modified to explain the response of pullets to two opposing changes in photoperiod given within 30 d of each other (pp. 16-18).

- The finding that sexual maturity is not advanced in egg-type pullets following transfer to a stimulatory photoperiod at a young age, despite an elevation in plasma LH concentration, because there is no photoinduced increase in FSH secretion (**Lewis *et al*., 1998*d*),** and that this is in some way a consequence of low circulating concentrations of oestradiol (**Lewis *et al*., 2001*a***).

- A definition of the effect of illuminance on age at first egg in egg-type pullets (**Lewis *et al*., 1999*a***).

- The demonstration that melatonin release only increases in the scotoperiod that is interpreted as the bird's night and not in darkness *per se* (**Lewis *et al*., 1989**).

- The conclusion that broiler breeders exhibit photorefractoriness (**Lewis *et al*., 2003*a***).

- The demonstration that the response of broiler breeders to a photoperiod between 10 and 13 h is markedly different from egg-type hybrids (**Lewis *et al*., 2004*a***), and the creation of a model to predict age at first egg in broiler breeders maintained on a constant photoperiod (**Lewis, 2006**).

- Creation of a model to predict sexual maturity in broiler breeders given a single change in photoperiod (**Lewis *et al*., 2007*g***).

- The demonstration that broiler breeders do not respond positively to increments from a mildly to a fully stimulatory photoperiod during the laying cycle (**Lewis *et al*., 2007*f***).

Manuscript under review

- Description of photoperiodic response curves for LH release and age at first egg in broiler breeders (pp. 6-7).

1. PHOTOSEXUAL MECHANISMS

1.1 Acquisition of photosensitivity

In an earlier investigation of the response of domestic fowl to photostimulation at very young ages, changes in plasma LH concentration and ovarian and oviducal growth, but not age at sexual maturation, were measured in typically grown dwarf broiler breeders (Dunn *et al*., 1990). A significant increase in plasma LH was noted 4 d after a transfer from 8 to 20 h at 3 weeks, but photostimulation failed to induce significant oviducal growth before 11 weeks and ovarian development before 15 weeks, indicating that the hypothalamo-pituitary axis was only partly functional at 3 weeks.

It was subsequently shown that, despite inducing significant rises in plasma LH concentration within 7 d of a transfer to long days, increments in photoperiod given to egg-type pullets at 5 or 6 weeks of age did not significantly advance AFE, and complete photoresponsiveness within a group of birds was not achieved until about 9 weeks (Lewis *et al*., 1994*b*, 1997*b*, 1998*d*, 2001*a*, 2002). In contrast, photoperiodically induced sexual maturation in typically managed broiler breeders was still minimal at 10 weeks, even though significant rises in plasma LH had been detected within 2 d of photostimulation, and acceleration of sexual maturity was not uniformly achieved in a flock of broiler breeders until 17 or 18 weeks (Lewis *et al*., 2003*a*, 2005*c*) (Figure 1.1).

In the period between the first and last bird becoming photoresponsive (between 6 and 9 weeks in egg-type and between 10 and 18 weeks in broiler breeders), a flock comprises two types of bird (Lewis *et al*., 2002, 2007*g*); one has its sexual development accelerated by a transfer to long days (responders) and the other matures as if held on long days (non responders). The mean AFE of a flock therefore depends on the proportion of birds within each category.
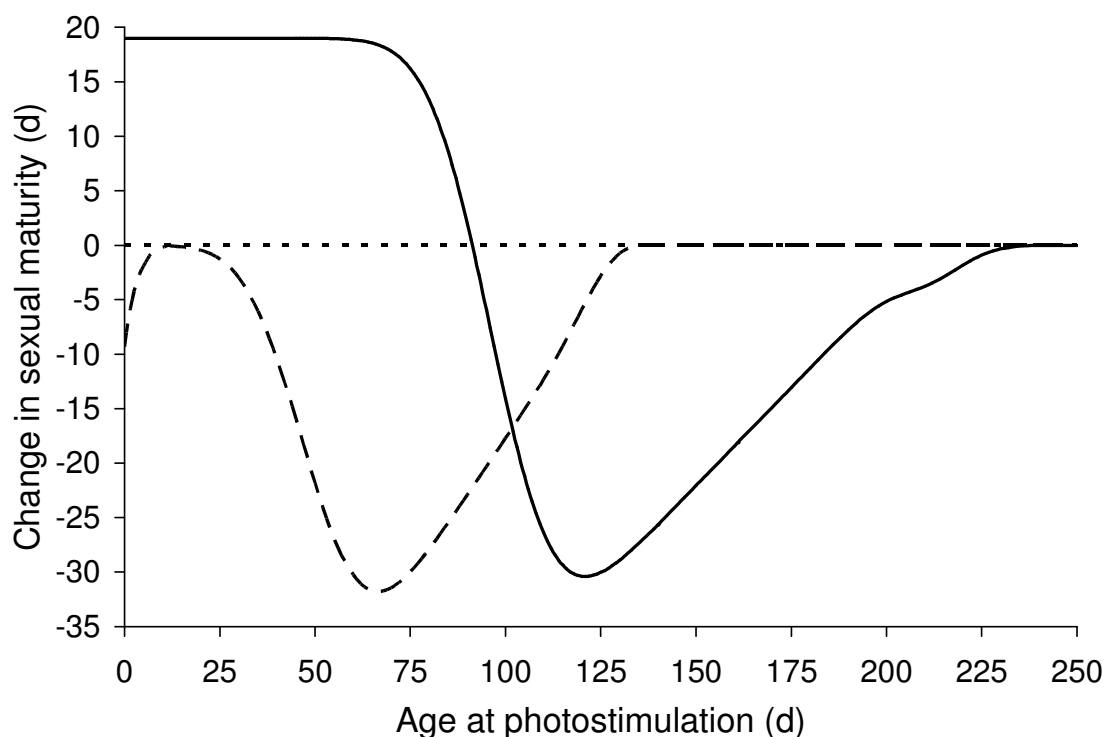
Figure 1.1 Effect of age at transfer from 8 to 16 h on mean change in age at sexual maturity in modern egg-type pullets (broken line) and female broiler breeders grown to a 2 kg body weight at 20 weeks (solid line) relative to constant 8-h controls (horizontal dotted line). Data from Lewis *et al.* (2002 and 2007*g*).
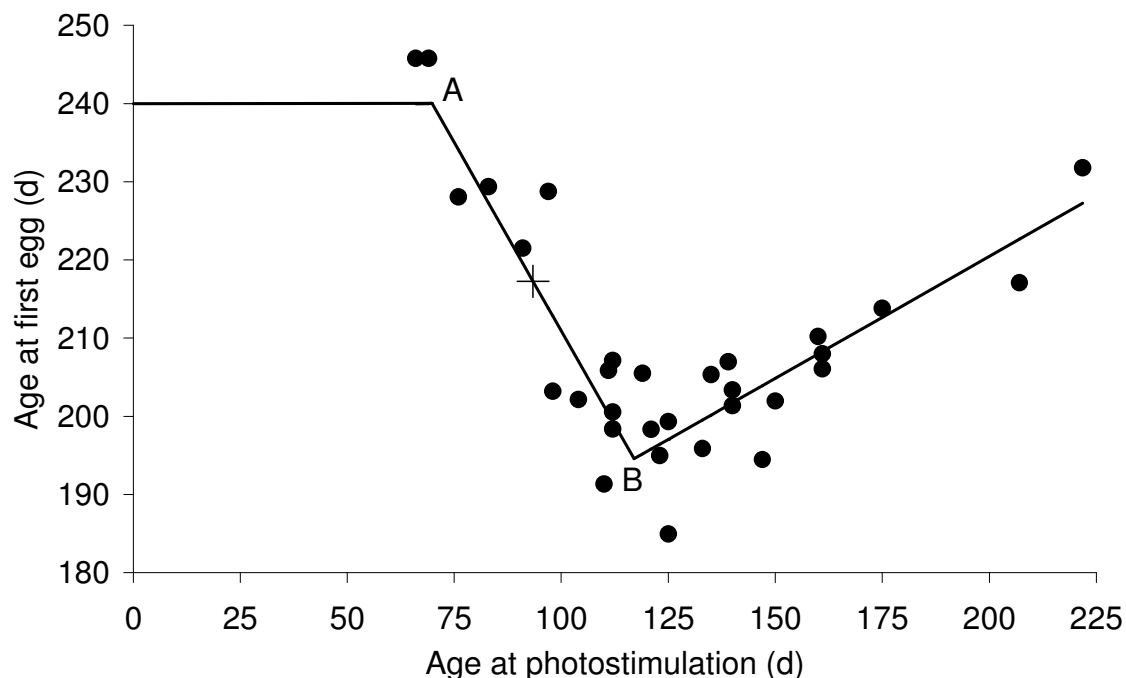
Figure 1.2 A hinge analysis to determine the mean age (+) for the acquisition of photosensitivity in broiler breeder females grown to a 2.0 kg body weight at 20 weeks when the first bird in a group matures at A and the last bird in a group matures at B (Lewis *et al.*, 2007*g*).

Lewis and Morris (2004) and Lewis *et al*. (2002, 2007*g*) assumed that the age at which different individuals in a flock acquire photosensitivity forms a normal distribution, with the proportion of responders at a given age determined by a mean and SD. Examples of the calculations for egg-type and broiler breeder pullets were given in Lewis *et al*. (2002) and Lewis *et al*. (2007*g*) respectively, and an example of the hinge analysis used to determine the mean for broiler breeders is shown in Figure 1.2.

1.2 Photorefractoriness

The difference in the ages at which egg- and meat-type fowl acquire photosensitivity is, in part, a consequence of a disparity in the degree to which each genotype exhibits photorefractoriness; a condition in which an animal is unable to respond positively to an otherwise stimulatory photoperiod. Intense genetic selection for egg production has virtually eliminated the condition from modern egg-laying pullets (Morris *et al*., 1995), but it is still manifest in broiler breeders (Lewis *et al*., 2003*a*). Although modern strains of egg-laying domestic fowl minimally exhibit photorefractoriness, they still need about 5 weeks to become photoresponsive; which probably reflects the time required for the hypothalamo-pituitary-ovarian to reach maturation (Lewis *et al*., 2001a). Whilst juvenile photorefractoriness can be dissipated in exotic avian species and domestic turkeys by a 2-month exposure to short days (Follett, 1991; broiler breeders, in contrast, are not fed *ad libitum*, and the consequential curb on growth is associated with a much slower acquisition of photosensitivity and a 2-d delay in mean AFE for each 100-g reduction in body weight at 20 weeks of age (Lewis, 2006; Lewis and Gous, 2006*a,b*; Lewis *et al*., 2005*a,b*, 2007*c,g*). Support for the view that the disparity between the rates at which turkeys and broiler breeders dissipate photorefractoriness is due to the difference in their feeding systems (turkeys full-fed, broiler breeders restrict-fed), and not to any genetic difference between the species for the time required to become photosensitive, was provided by

Lewis *et al*. (2007*c*). In a study, in which the degree of feed-restriction was markedly relaxed to allow the birds to reach a mean body weight of 2.0 kg for photostimulation at 75 d of age, mean AFE was advanced by 82 d relative to constant short-day controls. However, AFE was only advanced by 34 d when the birds were fed *ad libitum* and transferred to long days at 45 d, suggesting that broiler breeders, like other species, may also require about 2 months of short days to dissipate photorefractoriness when fed *ad libitum*.

A further factor affecting the age at which a broiler breeder achieves photosensitivity is the photoperiod to which it is exposed during the rearing phase. Farner and Follett (1966) suggested that there was a direct correlation between the rate of dissipation of photo-refractoriness and the rearing daylength; however, Lewis *et al*. (2004*a*) concluded that, rather than the relationship being linear, it was inversely proportional to the stimulatory competence of the photoperiod. Thus, broiler breeders maintained on very long days mature before birds held on shorter though more stimulatory photoperiods (Figure 2.3).

1.3 Maturation of the hypothalamo-pituitary-ovarian axis

The significant increase in LH release observed in pullets following photostimulation at various ages between 3 and 6 weeks, be they egg- or meat-type genotypes, but minimal effect on the timing of sexual maturation, indicated that the neuroendocrine mechanisms which control gonadotrophin release and ovarian follicular development are not fully functional at these young ages (Dunn *et al*., 1990; Lewis *et al*. 1994*b*, 1997*b*, 1998*d*). It was then demonstrated that photoperiodic increments given to modern egg-type pullets at 8 or 9 weeks induce significant increases in both LH and Follicle Stimulating Hormone (FSH) secretion and advance gonadal development; but that photostimulation at 5 or 6 weeks fails to have any effect on FSH release or sexual maturation (Lewis *et al*., 1998*d*, 1999*b*) (Figure 1.3). It therefore appeared that stimulation of FSH release was essential for
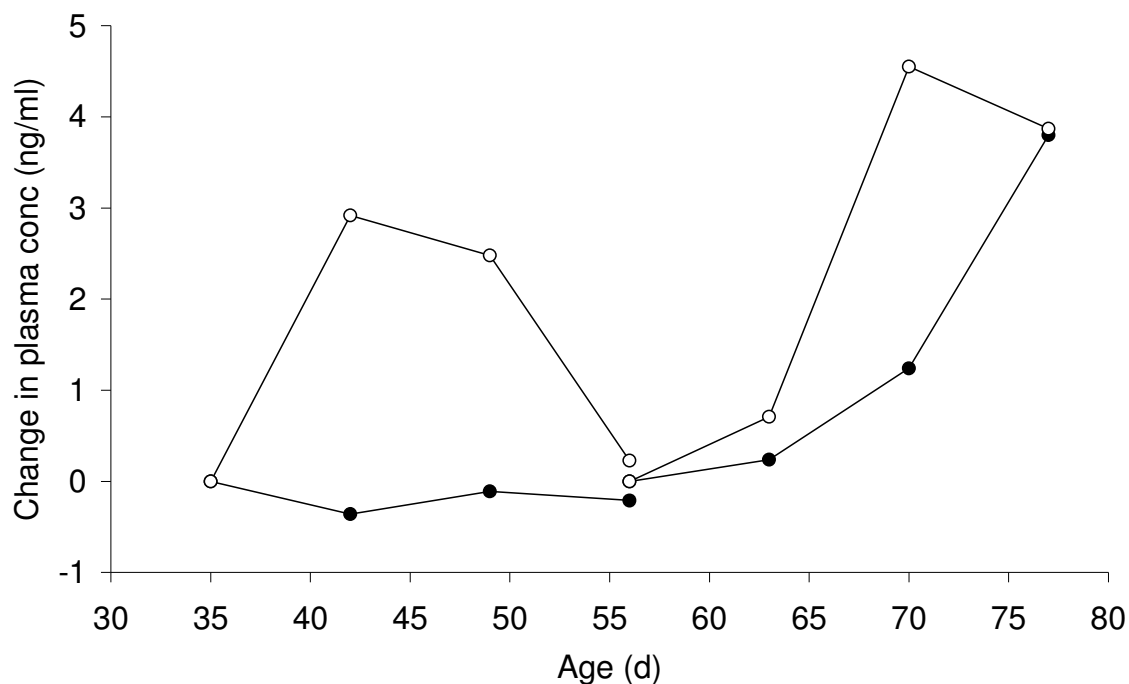
Figure 1.3 Changes in plasma LH (○) and FSH (●) concentrations in egg-type pullets transferred from an 8 to a 14-h photoperiod at 35 or 56 d of age (from Lewis *et al*., 1998d).

a successful photoperiodic response. Dunn (1997) questioned whether oestrogen was a required for maturation of photoinduced gonadotrophin responses. Subsequently, Lewis *et al*. (2001*a*) demonstrated that increasing plasma oestrogen levels in egg-type pullets, by injecting oestradiol benzoate on alternate days from 6 d before to 6 d after a transfer from 8 to 16 h at 34 d, significantly raised plasma LH concentration and tended (*P*=0.15) to accelerate gonadal maturation. In a second study, exogenous oestradiol increased circulating concentrations of both LH and FSH but depressed pituitary LH and FSH contents in pullets stimulated at 34 d (Dunn *et al*., 2003). Surprisingly, exogenous oestradiol in the first study had no effect on plasma gonadotrophin concentrations when photostimulation occurred at 44 or 54 d, and significantly delayed AFE relative to birds photostimulated but injected with vehicle (arachis oil) only when given at 54 d. In the second study, oestradiol blocked photoinduced LH and FSH release at 54 d but did not block the stimulatory effect of photostimulation on pituitary FSH content.

1.4 Photoperiodic response

Photosensitive domestic fowl respond to a transfer from a non-stimulatory short day to a stimulatory long day by increasing their secretion of gonadotrophins and then, in response to elevated plasma FSH and to a lesser extent increased LH release, initiate rapid gonadal development. Although the effect of a transfer from short to long days on gonadotrophin release has been studied in egg-type and meat-type genotypes of fowl (e.g., Wilson and Cunningham, 1980; Dunn and Sharp, 1990), the studies have not been in depth nor has photostimulation been at ages typically employed by the commercial poultry industry. Rates of gonadal growth have been measured in male quail (e.g., Follett and Maung, 1978; Follett, 1981; Urbanski and Follett, 1982); but there have been no studies of the effect of transfers at commercially typical ages to different final photoperiods on sexual maturation in female fowl, and the relationship between the response curves for LH release and AFE has not been established.

Unpublished data from a study conducted by the author at the University of KwaZulu-Natal were used to produce photoperiodic response curves for changes in plasma LH concentration 4 d after photostimulation (Figure 1.4) and mean AFE (Figure 1.5) in broiler breeder females photostimulated at 20 weeks. It was concluded that the responses were similar, that the point at which the responses began to rise steeply (critical daylength) was 9.5 h, and that the asymptote (saturation daylength) was 13.h in each curve. Functionally, however, the minimum final photoperiod to achieve a significant increase in LH secretion and an advance in AFE was between 11 and 11.5; hence, the minimum daylength to which commercial broiler breeders should be transferred when they are photostimulated.
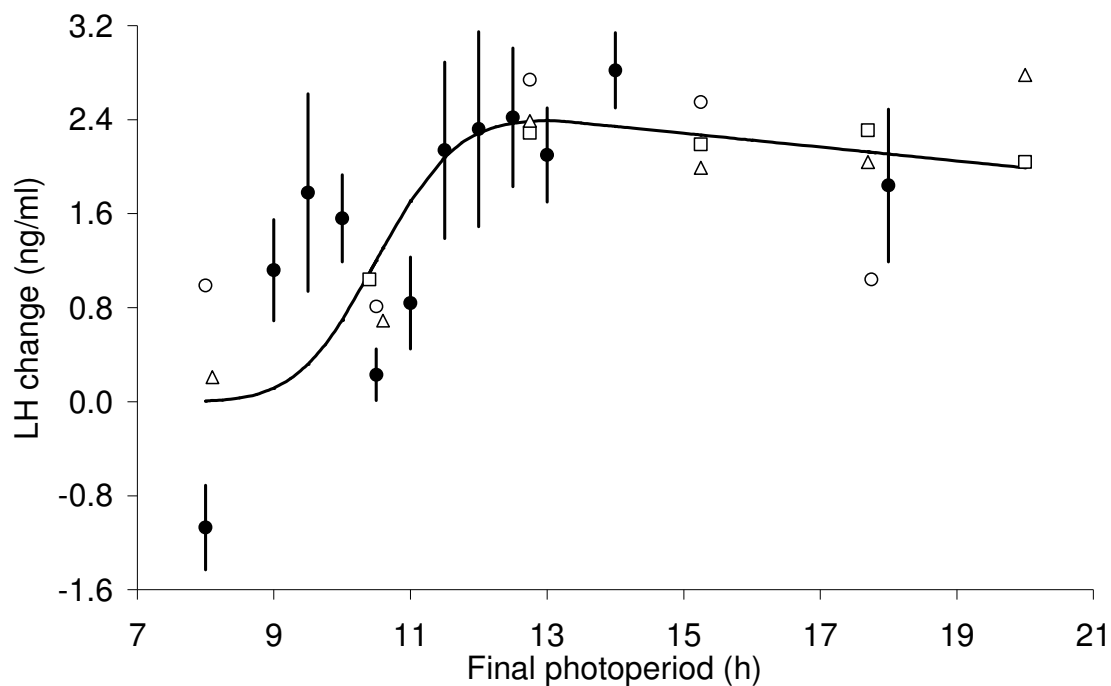
Figure 1.4 Regression of mean change (±SEM) in plasma LH concentration between 3 d before and 4 d after photostimulation on final photoperiod for broiler breeders grown to a mean body weight of 2.1 kg at 140 d and transferred from an 8-h photoperiod at 144 d (●), and for restrict-fed normal size broiler breeders in a preliminary study (○), and from Dunn and Sharp (1990) for *ad-libitum* fed (□) and restrict-fed (Δ) dwarf broiler breeders photostimulated at 56 d.
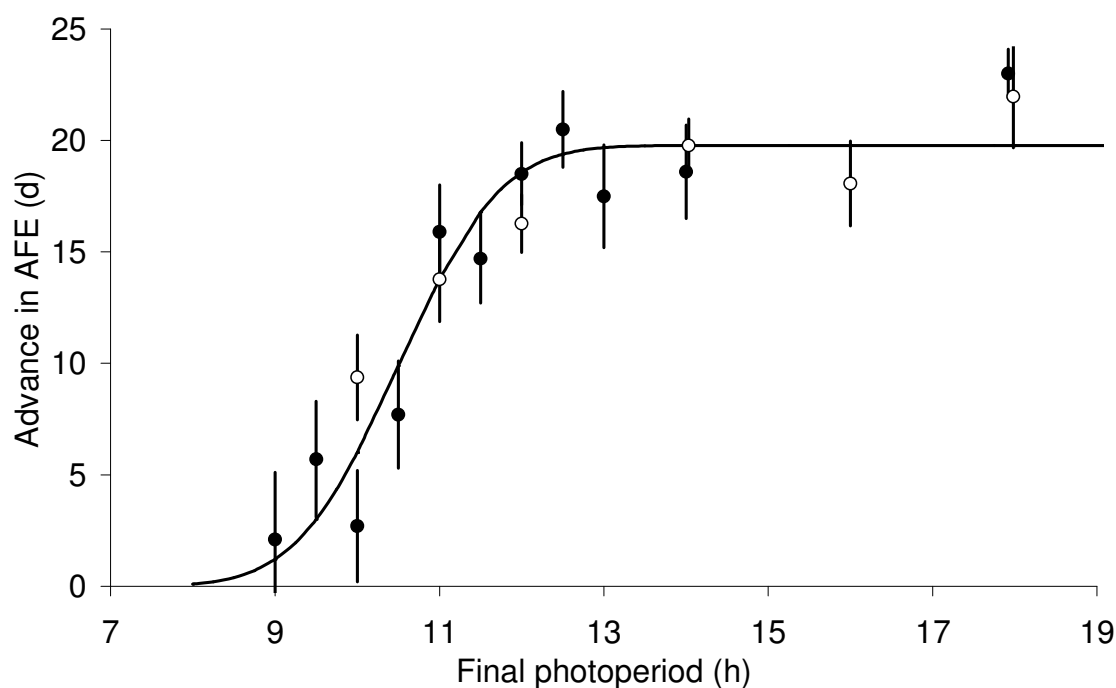
Figure 1.5 Regression of advance in mean age at first egg (±SEM) (●) and Lewis and Gous (2006*b*) (○) on final photoperiod for broiler breeders grown to a mean body weight of about 2.1 kg at 140 d and transferred from an 8-h photoperiod at 140 or 144 d.

1.5 Hormonal changes as predicators of sexual maturation

In previous sections we have seen that photostimulation at very young ages induces a significant increase in plasma LH concentration but has minimal influence on sexual maturation; yet photostimulation at older ages, when a bird is photosensitive, significantly advances AFE but, due to the negative feed back of rising gonadal steroid concentrations, has a markedly reduced effect on LH secretion. Classically, changes in plasma LH concentration have been used to measure a bird's response to photostimulation, but, because of these contradictory responses, photoinduced changes in plasma LH have been poor predictors of AFE in both egg- and meat-type genotypes (Lewis *et al*., 1994*b*, 1998*d*, 2005*c*). Notwithstanding the unquestionable poor correlation of change in plasma LH with change in mean AFE when groups of birds have been transferred to a stimulatory photoperiod at different ages, the unpublished findings of the study of the photoresponse curves for plasma LH concentration and AFE in photosensitive broiler breeders transferred to various final photoperiod at 20 weeks (discussed above and Figures 1.3 and 1.4) showed that there was a significant regression (P=0.015) of change in plasma 4 d after photostimulation and advance in mean AFE.

No sensitive and specific radioimmunoassay for chicken FSH was available at the time of the initial study of the photoresponse in egg-type pullets conducted by the author (Lewis *et al*., 1994*b*), but its subsequent availability (Krishnan *et al*., 1993) permitted measurements of FSH in plasma samples retained from earlier experiments. The findings of these assays showed that changes in plasma FSH concentration during the 14 d after egg-laying strains of pullets had been transferred to a stimulatory photoperiod were significantly correlated with (P<0.001), and much more accurate predictors of, mean AFE than previously reported changes in LH (P=0.068) (Lewis *et al*., 1998*d*, 1999*b*). However, changes in plasma FSH within 2 d of broiler breeder pullets being transferred from 8 to 16 h at 7 or 18 weeks were poorly correlated (P=0.94) with differences in mean AFE

(Lewis *et al*., 2005*c*). Notwithstanding that significant change in plasma LH had been detected within 2 d of photostimulation, the second sampling may simply have been taken too soon for rising FSH secretion to be detected (layer strains were sampled after 14 d), especially as they must have risen eventually in the birds given a photoperiodic increment at 18 weeks to have advanced mean AFE by 5 weeks (Lewis *et al*., 2003*a*). This may also have been the reason, in a separate study, for the absence of a significant correlation between change in mean AFE in two strains of egg-laying hybrid and change in plasma FSH induced by a change in illuminance at 9 or 16 weeks (Lewis *et al*., 2005*d*).

1.6 Melatonin and its involvement in photoperiodism

Melatonin is a hormone synthesized in the pineal gland and retina of birds during the hours of darkness in response to the activity of serotonin-N-acetyltransferease (Binkley *et al*., 1973). During the day, the light-induced production of dopamine within the retina suppresses the production of serotonin in the photoreceptors and, as a consequence, suppresses the biosynthesis of melatonin. The switch between day and night mode, which takes place over a remarkably narrow illuminance range of 0.1 to 4 lux (Morgan *et al*., 1995), and the existence of melatonin receptors in the hypothalamus and anterior pituitary (Murayama *et al*., 1997, 1998) makes the circadian cycle of melatonin release a potential provider of photoperiodic time measurement to the hypothalamo-pituitary axis.

Lewis *et al*. (2006) tested the hypothesis that modulations of the melatonin diurnal cycle, without a change in the lighting regimen, could effect changes in the rate of sexual maturation in egg-type pullets. Exogenous melatonin was incorporated in an experimental diet and access to it or a normal diet restricted to the final 7 h of a 14-h photoperiod to raise circulating melatonin concentration in experimental birds and hopefully, despite the illumination, dupe them into believing that this phase of the light-dark cycle formed part of their night; thus inducing it to respond as if to a 7L:17D regimen rather than the actual

14L:10D. The birds were switched between supplemented and normal diets at different times to mimic increases and decreases in photoperiod at various ages. Data from literature for short-term studies had indicated that a dose of 25 mg/kg of diet would achieve normal nocturnal physiological concentrations of circulating melatonin. However, the prolonged feeding of the experimental diet in this study led to atypically high levels of plasma melatonin during the first 7 h of illumination; a period when the birds were without feed and when circulating melatonin should have been minimal. It was postulated that the abnormally high concentrations of melatonin at a time when light-induced dopamine would normally have suppressed its biosynthesis were caused by a combination of endogenous and exogenous melatonin accumulating to such a level that the liver was unable to remove it before the experimental diet again became available; and so the constant elevation of melatonin would have prevented any interpretation of a change in photoperiod when experimental and normal diets were switched. Although the study failed to unequivocally demonstrate that melatonin provides photoperiodic information to the hypothalamus, the 6 to 11-d significantly later maturity of all groups given exogenous melatonin, relative to controls given 14 h illumination and normal diets throughout the trial, indicated that melatonin does exert some influence over hypothalamic activity and gonadal development.

Studies of the diurnal rhythm of melatonin release have invariably involved the use of conventional light-dark cycles, and so the effects of day and night on its synthesis were synonymous with the effects of light and darkness. This conundrum was elucidated by Lewis *et al*. (1989) in a study of melatonin release in laying hens exposed to either a conventional 14L:10D or an asymmetrical interrupted 8L:4D:2L:10D regimen. Blood samples were taken 6, 11, 13 h after the start of the main photoperiod and 3 h after the start of the 10-h scotoperiod and, at each sampling time, there was no significant difference in plasma melatonin concentration between the solidly and intermittently illuminated groups
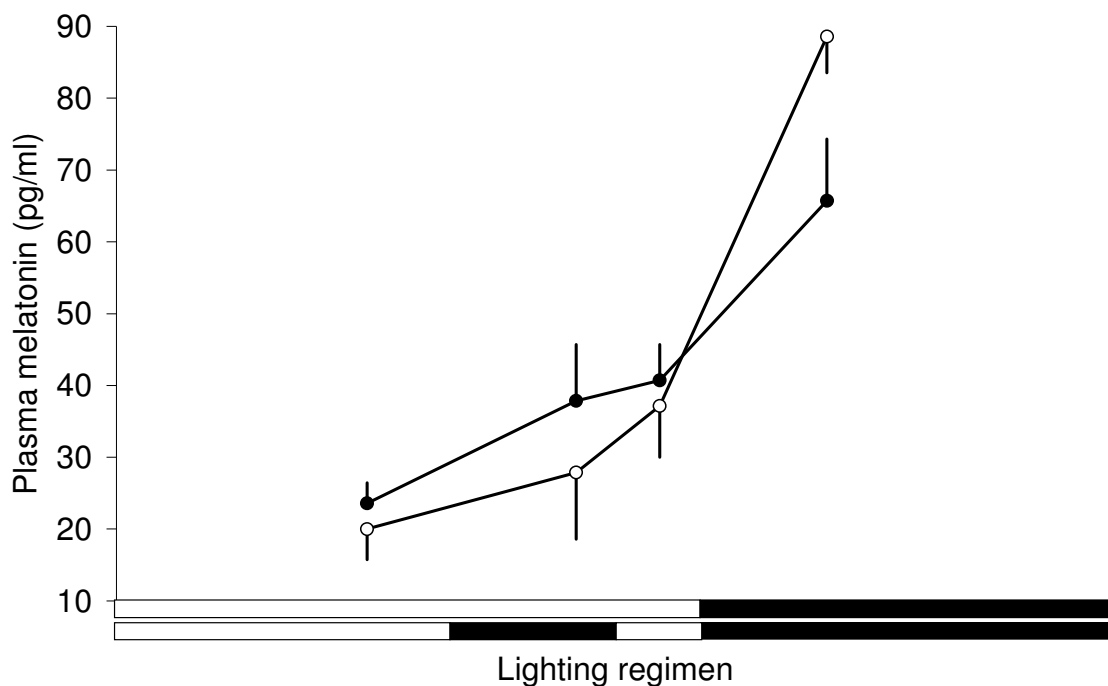
Figure 1.6 Plasma melatonin concentrations at 6, 11, and 13 h after the start of the main photoperiod and 3 h after the start of the 10-h scotoperiod in hens subjected to a 14L:10D (●) or an 8L:4D:2L:10D (○) lighting regimen (Lewis *et al*., 2001*b*).

(Figure 1.6). In particular, the similarity of plasma melatonin concentrations 11 h after dawn, when the intermittently illuminated birds were in darkness and the conventional birds were in light, demonstrated that melatonin synthesis is only elevated during scotoperiods that are interpreted as night and not during darkness *per se*, and that the diurnal rhythm of synthesis is in response to the bird's subjective day and night.

The addition of an 8-h period of very dim light (0.1 lux) to a normal 7-lux photoperiod advanced the melatonin rhythm of 24-week old domestic pullets by 5 h when it preceded the main photoperiod, and retarded the rhythm by 5 h when it followed the photoperiod (Lewis *et al*., 2001*b*). In contrast, a 2.4-h earlier mean oviposition time for birds given the dim light before the main photoperiod, but no difference relative to un-supplemented controls when given after the main 8 h, showed that the biological clocks controlling melatonin synthesis and the ovulatory cycle are differentially affected by changes in lighting conditions.

1.7 Carryover effect

Carryover effect and flywheel effect are terms for a phenomenon that allows photoinduced activity of the hypothalamo-pituitary-gonadal axis to continue after a period of stimulatory illumination has ended (Farner *et al*., 1953). The phenomenon was successfully demonstrated in white-crowned sparrows (Follett *et al.,* 1967) and quail (Follett *et al.,* 1981) by mixing short and long days. In the quail, ovarian and oviducal weights were only slightly lower in experimental birds given alternating long and short days, or one long day followed by three short days, than in long-day controls. In another study, testicular mass in house sparrows previously exposed to a stimulatory photoperiod was unchanged 4 weeks after they had been transferred to complete darkness (Farner *et al.,* 1977).

Lewis (1987) concluded from his studies of asymmetrical interrupted lighting regimens that the carryover effect explained why laying hens were as responsive to such programmes as they were to the fully illuminated equivalents. For example, locomotor rhythms, diurnal feeding activity, melatonin release, rates of lay, phase setting of the ovulatory cycle, and oviposition timing for birds given an 8L:4D:2L:10D regimen were similar to those for birds given a conventional 14L:10D cycle.

Lewis *et al*. (1997*c*) studied the phenomenon in egg-type growing pullets using a continuously repeating 'saw-tooth' cycle of twelve 30-min increments in photoperiod between 8 and 14 h and a single abrupt decrease back to 8 h; controls were maintained on 8, 11 (mean daily illumination for 8 to 14 h birds) or 14 h. Mean AFE for the experimental birds was similar to constant 14-h controls, 7 d later than birds held on 11 h, but 12 d earlier than those maintained on 8 h. The findings showed that the birds neither responded to the experimental regimen as one of continuously increasing photoperiods nor as a constant photoperiod equivalent to the mean daily illumination. Instead they showed that once a bird has received a maximum of 14 h (repeated every 14 d), it does not need to be maintained on it for gonadal development to proceed as if it had been.

1.8 Photoinducible phase

Birds are only sexually responsive to light for a limited period of the light-dark cycle termed the photoinducible phase (PIP); a period within the internal biological cycle when the hypothalamus can be excited by light (Pittendrigh, 1966). The first evidence of the involvement of circadian rhythms in avian photosensitivity came from resonance experiments conducted by Hamner (1963) in male house finches. Subsequently, Follett & Sharp (1969) demonstrated a PIP of about 4-h duration lying 12-16 h after the beginning of a main 6-h photoperiod in quail given a 15-min light pulse at various locations during their 18-h night. The amount of illumination required during PIP to induce maximum testicular growth in quail has been reported to vary between 1 h (Follett & Milette, 1982) and 4 h (Siopes and Wilson, 1980). Follett & Milette (1982) also concluded that the amount of illumination required for the maintenance of testicular mass in mature quail was significantly less than that required to initiate growth in immature birds.

Lewis and Perry (1988) postulated that if the response of domestic fowl to PIP was similar to quail, savings in energy usage (feed and electricity) could be made, without compromising reproductive performance, by reducing the total amount of daily illumination. In an empirical study, sexually mature laying hens were subjected to various interrupted lighting programmes which involved a mixture of long and short days (potentially using the carryover effect). During short days, the 8-h photoperiod was removed from an 8L:4D:2L:10D regimen to leave only 2 h of illumination located within PIP; it was assumed that PIP was located between hours 10 and 14 of a conventional 14L:10D regimen and that 50% illumination of PIP would be sufficient to sustain reproductive performance. The birds had previously received 31 weeks of exposure to the 8L:4D:2L:10D asymmetrical regimen, which would they would have interpreted as a 14-h 'day' and 10-h 'night' (Lewis, 1987), and were introduced to the experimental treatments at 49 weeks of age. The protocol involved withdrawal of the 8-h photoperiod for one cycle

(thus 2L:22D) followed by 6 cycles of 8L:4D:2L:10D in one group, and two cycles of 2L:22D followed by 5 normal cycles in another. The ratio of long to short days was progressively narrowed to 1 long:1 short, and finally to 10 consecutive short days in the first group, and to a repeating 1 long:4 short in the second. At no stage of the study did rate of lay, egg weight, or mean time of oviposition for the experimental groups differ from that of controls maintained on 8L:4D:2L:10D. However, *ad libitum* feed intake progressively reduced to 99 g/d (controls 122 g/d) and the conversion of feed into egg mass improved by 23% in the first group, and feed intake decreased to 111 g/d and feed conversion improved to 1.11 of controls in the second group.

The findings of another empirical study, reported at the *VIIIth European Poultry Conference* (Lewis and Perry, 1990), showed that radio noise could be used to replace the first 8 h of a 12-h conventional photoperiod, leaving 4 h of light to fully illuminate PIP. The hypothesis was that, for satisfactory reproductive performance, light need only be provided during PIP and that other environmental cues, such as noise, could be used to encourage the birds to continue to respond to the regimen as if to a long day. Egg output was similar for experimental and 12L:12D control birds during the 12-week study; but with a significant reduction in feed intake and a consequential improvement in feed conversion efficiency. However, a 4-h advance in mean oviposition time for the experimental group suggested that the ovulatory cycle was phase-set by the period of illumination and did not involve PIP; a similar affect, discussed on p. 11, was observed when laying hens were given a main 8-h photoperiod followed by 8 h of supplementary dim light (Lewis *et al*., 2001*b*). Evidence to support the hypothesis that the noise acted as a zeitgeber to maintain a long-day response was the drop in egg production that occurred when the noise was withdrawn, presumably because PIP had phase-shifted backwards into the scotoperiod and was therefore no longer illuminated, leaving the birds to respond only to the non-stimulatory 4-h photoperiod.

Whilst the findings demonstrated that non-photic cues can be used successfully to anchor PIP and encourage a feed intake sufficiently large to support maximum egg production, development and use of these energy-efficient programmes by commercial poultry industries has been prohibited in areas of the world where animal welfare regulations stipulate that laying hens must be given at least 8 h of daily illumination.

In contrast to the attempted anchoring of PIP in sexually mature pullets by the replacement of existing light with radio noise, as described above, Lewis *et al*. (2005*e*) played radio noise for 7 h in the period of darkness immediately preceding a non-stimulatory 7-h photoperiod from 10 weeks of age to assess whether this would create a stimulatory daylength for sexually immature pullets. The treatment resulted in a 13-d advance in mean AFE relative to birds maintained on a 7-h photoperiod but not given radio noise. Plasma melatonin concentrations in blood samples taken during darkness in the middle of the noise period from experimental birds were not significantly different from 'no-noise' controls, and so it seems that the experimental birds had not combined 7 h of noise with 7 h of light to make a 14-h subjective day; Lewis *et al*. (1989) had previously reported that melatonin synthesis is not suppressed in darkness that forms part of a subjective day (p. 11). It was therefore postulated that the noise had phase-advanced PIP, located in the night for birds on short days, to a point where it had become partially illuminated by the end of the hitherto non-stimulatory 7-h photoperiod, thus making it mildly photoinductive. The 7-h short day had not been interpreted as a fully stimulatory 14-h day, because data from other studies had shown that a transfer to long days at 10 weeks of age is likely to advance mean AFE by at least 5 weeks (e.g., Lewis *et al*., 1996*b*, 2001*b*).

1.9 Temporary transfer to long days

The provision of a single long day or light pulse during the PIP of a short day to immature birds has been reported to induce a significant rise in gonadotrophin (LH) release within 24 h (e.g., intact quail, Follett *et al*., 1977), and a permanent transfer to a stimulatory daylength to produce a 2 to 3-fold in plasma LH in egg-type pullets within 1 to 3 d (Wilson, 1982). However, most of these earlier studies were terminated after changes in LH concentration had been determined and did not continue through to sexual maturation; indeed some used gonadectomised birds. Nevertheless, the knowledge that one long day was sufficient to induce a photosexual response has been the reason why the world's poultry industries ensure that sexually immature pullets are neither intentionally nor accidentally exposed to a long day prior to the planned age for photostimulation.

Lewis and Gous (2004) demonstrated that transfers from 8 h to 10, 12 or 14 h for 1 or 2 d at 11, 13 or 15 weeks of age had no effect on the timing of sexual development in egg-type pullets, and had no detrimental effect on their response to a subsequent permanent transfer to long days. In a follow-up study, Lewis and Gous (2006*e*) showed that pullets could be given up to 6 d of temporary exposure to 14-h photoperiods without any apparent effect on sexual maturation (Figure 1.7). An extrapolation of data for birds given ≥ 6 long days suggested that at least 20 long days may be required to maximally advance AFE.

Lewis *et al*. (2003*b*) had concluded that when a bird is given two opposing changes in photoperiod, the first change alters the bird's physiology so that it responds to the second as if it were applied at the bird's 'physiological age' rather than its chronological age; thus, when the initial change is an increase, the physiological age of the bird will be advanced (potentially closer to maturity) so making it more sensitive to a subsequent decrease in photoperiod than would be expected by reference to its chronological age. However, the data published by Lewis and Gous (2006*e*) were very poorly correlated with predictions of
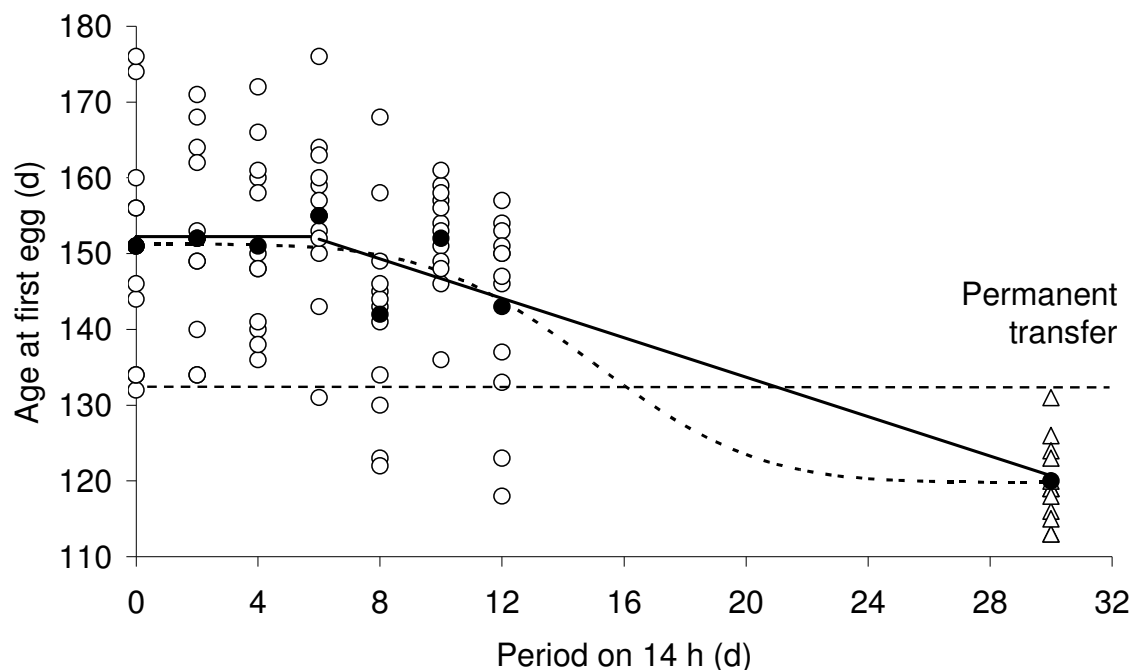
Figure 1.7 Individual ages at first egg (○) and treatment means (●) for egg-type hybrids temporarily transferred from an 8- to a 14-h photoperiod for 2, 4, 6, 8, 10 or 12 d from, or permanently transferred to 14 h at (△), 80 d of age (Lewis and Gous, 2006*e*). An extrapolation of the regression of mean data for groups given 6, 8, 10 or 12 long days suggested that 30 long days were required to maximise the photosexual response. The dotted line is the predicted response using expected changes in plasma FSH during the 30 d immediately following a permanent transfer from 8 to 14 h.

Table 1.1 Actual (Lewis and Gous, 2006*e*) and predicted mean AFE in egg-type pullets temporally transferred from 8 to 14 h at 80 d for 2, 4, 6, 8, 10 or 12 d, or given a single change from 8 to 14 h using models that (a) included or (b) did not include an adjustment for 'physiological age', and (c) used anticipated changes in plasma FSH concentration.

Temporary period on 14 h (d)	Actual mean AFE (d)	Prediction with a change in physiological age (d)	Prediction with no change in physiological age (d)	Prediction using amended model (d)
0	151.3	-	-	151.3
2	152.3	137.8	156.0	151.3
4	151.4	134.1	156.9	151.2
6	155.3	130.8	157.8	150.8
8	142.0	127.9	158.7	149.8
10	152.3	125.6	159.5	147.6
12	143.3	123.8	160.4	143.8
∞ (8 to 14 h)	120.0	-	-	119.8

mean AFE using the Lewis *et al*. (2003*b*) model and could not be explained by simply combining responses to the two photoperiodic changes without adjustment for 'physiological age' (Table 1.1). This dilemma prompted the hypothesis that ovarian and oviducal development in egg-type pullets given two opposing changes in photoperiod, but with only a small interval between them, is in response to the change in circulating FSH concentration induced by the increase in photoperiod, and that a return to short days will only minimally affect sexual maturation because the effect of a decrease in photoperiod on FSH release is negligible at this time (Lewis *et al*., 1998*d*). Photoinduced increases in FSH secretion following a transfer to long days are initially small, but then rise rapidly between 7 and 21 d, and eventually peak after about 28 d. As a consequence, AFE for the birds given ≤ 6 long days in the Lewis and Gous study was little different from birds held on short days, but then progressively advanced as longer periods of rising plasma FSH concentration were experienced. A re-analysis of the suggestion of Lewis and Gous (2006*e*) that 20 long days were required to maximise the response to a transfer from 8 to 14 h, using an extrapolation of means rather than data for the first and last maturing birds, indicated that 30 d was a more likely figure (Figure 1.7); a period that more closely matches that required for FSH release to reach its apex. It is suggested, therefore, that the model of Lewis *et al*. (2003*b*) for the response to two opposing changes in photoperiod is only applicable when an interval between opposing changes in photoperiod is greater than 30 d, by which time elevations in plasma FSH induced by the initial increment are naturally starting to subside (Lewis *et al*., 1998*d*).

Practical application

These findings have very important practical commercial implications because they indicate that temporary extensions of a photoperiod may be safely given during the rearing period without triggering an undesirable advance to the start of egg production or increased

risk of precocity. Such interruptions of a pre-planned lighting programme are often necessary to conduct emergency repairs to, or maintenance of, equipment, or to give extended feeding and drinking time when birds have endured protracted periods of transportation between the rearing and laying farms.

1.10 Ovulation and oviposition times

Constant photoperiods

Pre-ovulatory surges of LH are restricted to a centrally located 8- to 10-h period in the bird's night called the 'open period' (Wilson and Cunningham, 1984), and can be phase-shifted by changes in dawn and, more particularly, dusk (Bhatti and Morris, 1978). Oviducal transit times vary marginally between consecutive eggs with a sequence, and so changes in oviposition time are overt indicators of temporal changes in the open period and ovulation. There had been many reports of the effect of photoperiod on oviposition time in laying hens (e.g., Lanson and Sturkie, 1958; Mongin *et al*., 1978), but most had used only one breed; invariably White Leghorn (WL) or a WL cross.

Lewis (1987) reported oviposition times for four genotypes of modern brown-egg hybrids and noted that, whereas there was little variation among breeds, mean oviposition time (MOT) for a given photoperiod was about 1.5 h earlier than previously recorded in WL hens. Lewis *et al*., (1995) studied oviposition times in modern brown- and white-egg hybrids exposed to 8, 10, 13 or 18-h photoperiods and noted that white-egg hens laid eggs 1.2 to 1.4 h later than the brown-egg hens given the same lighting regimen; this was attributed to genetic differences in the phase setting of the 'open period'. In each breed, MOT was delayed by about 0.5 h for each 1-h extension of the photoperiod. The brown-egg hybrid commenced egg production more abruptly and had a more concentrated period of egg laying when exposed to 18 h of light than when given an 8, 10 or 13-h daylength, or the white-egg strain under any photoperiod. This abrupt start to egg laying was

subsequently demonstrated to be a consequence of low concentrations of plasma melatonin towards the end of the antecedent photoperiod preventing a pre-ovulatory surge of LH and, in turn, an ovulation (Nøddegaard, 1996).

Lewis *et al*. (2004*b*) investigated the effect of various photoperiods on time of egg laying in broiler breeder hens and observed that for a given lighting regimen, MOT occurred 1 h later than for a white-egg hybrid and 2.5 h later than for a brown-egg hybrid. However, the 0.49-h delay in MOT for a 1-h extension of the photoperiod compared remarkably well with changes in MOT seen in other studies, indicating that the mechanism for phase setting of the open period is probably common to all genotypes of domestic hen.

A meta-analysis of the many sources of data for MOT, with differences from the brown-egg hybrid studied by Lewis *et al*. (1995) removed by least squares, showed that MOT was curvilinearly related to photoperiod between 1 and 23 h (Figure 1.8), but that a linear regression, with its slope described by the equation MOT = -4.36 +0.51*p* (*p* = photoperiod (h)), could be satisfactorily fitted over the more practical range of 6 to 18 h (p. 30 in *Poultry Lighting the theory and practice* by Lewis and Morris, 2006).

Changing photoperiods

Morris (1973) stated that oviposition time was completely reset to the new lighting schedule within 4 d of hens being given a 6-h advance in the timing of a 14-h photoperiod, indicating that simply moving the complete photoperiod forward so that the lights come on before the birds currently commence egg laying does not result in them permanently laying later relative to dawn. However, the response to lengthening a photoperiod by turning lights on earlier in the day without changing the time of lights-out (dusk being more potent than dawn for phase setting of the ovulatory cycle) had not been reported.

Lewis *et al*. (2007*d*) conducted three studies of the effect on MOT of (a) adding 4 h of light immediately before or after an 8-h photoperiod, to create a 12-h day, before the birds
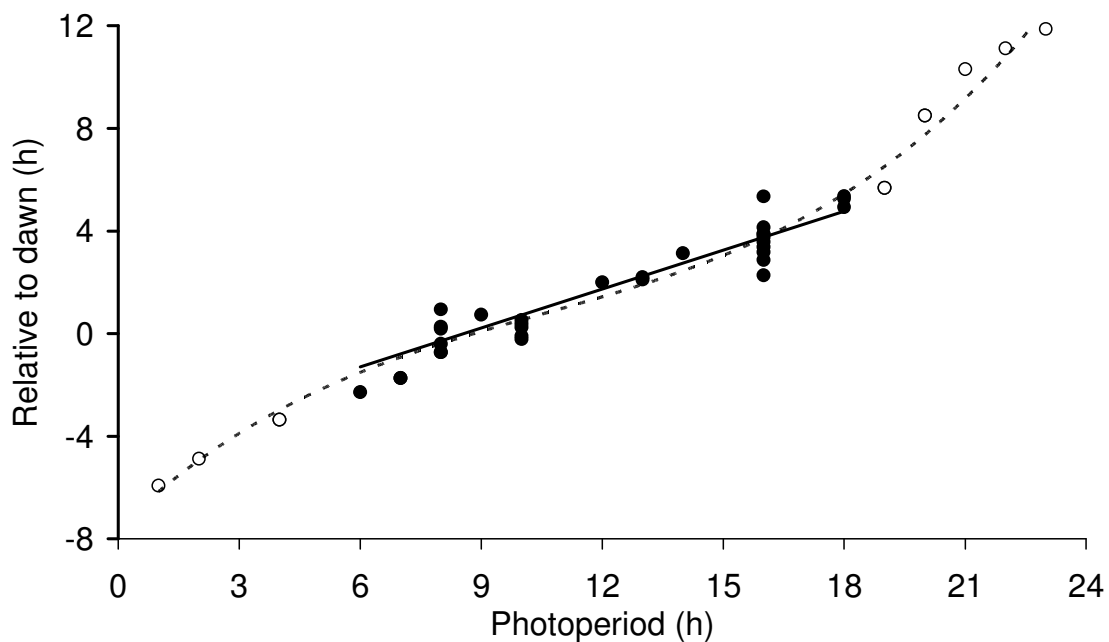
Figure 1.8 Mean oviposition time relative to dawn for brown-egg and white-egg laying hens exposed to various photoperiods between 1 and 23 h. The dotted curvilinear regression is for all data and the solid linear regression line for photoperiods between 6 and 18 h (Lewis and Morris, 2006 - book).

had become sexually mature, (b) using the same methods to further increase daylength to 16 h after the birds had commenced egg production, and (c), moving a complete 12- or 16-h photoperiod forwards or backwards by simultaneously advancing or delaying dawn and dusk. The findings showed that an advance of dawn produced a similar size shift in MOT to a delay in dusk, and an increase in photoperiod, irrespective of method, delayed egg laying by about 0.5 h for each 1-h extension. Moving the complete photoperiod forward or backward by simultaneously moving dawn and dusk only shifted actual MOT; its location relative to the new dawn was unchanged.

1.11 Body weight changes immediately prior to first egg

Typically, *ad libitum*-fed brown-egg hybrids increase their body weight by about 10-12 g/d during the second half of the rearing period. However, in the two weeks immediately preceding the laying of first egg, a pullet undergoes the final rapid stages in the development of its reproductive organs, and almost doubles its daily weight gain (an ovary and oviduct frequently weigh in excess of 100 g at first egg). Lewis and Perry (1995*b*) concluded that the daily body weight gain in an individual pullet during the final 20 d of sexual maturation was independent of its age or body weight at first egg, and could be described by the following equation:

$$y = 9.24 - 4.66x + 0.452x^2 - 0.111x^3$$

where y = daily weight gain (g), and x = days prior to first egg. As soon as the first egg has been laid, fat-free somatic body weight plateaus, or, in some cases, transitorily falls during the days immediately following first egg.

The variation in individual ages at first egg within a flock is not the same at all maturities, and, in the breed regularly used during the authors' studies at the University of Bristol (ISA Brown), the SD of individual AFE was described by the equation:

$$y = 63.3 - 0.900A + 0.0036A^2$$

where y = SD (d), and A = mean AFE (d). On the assumption that the individual AFE within a group of birds form a normal distribution, an estimate of the proportion of birds maturing at the same time was produced, and this enabled predictions to be made for the development of mean body weight for a group of birds with a given mean AFE. The computations showed that the mean body weight of an early maturing group of pullets initially exceeds that of a later maturing group, due to its earlier rapid gonadal development, but that the later-maturing group eventually has a heavier body weight because it continues to grow and undergo rapid gonadal development at a time when somatic growth has virtually ceased in the early-maturing group.

1.12 Direct and indirect photoperiodic effects of a transfer to long days on gonadal development

In addition to stimulating the release of gonadotrophins, an increment in photoperiod encourages feed intake and accelerates body weight gain in *ad libitum*-fed photosensitive egg-type pullets (Lewis and Perry, 1989*b*; Lewis *et al*., 1996*d*). However, the study by Lewis *et al*. (1996*b*) demonstrated that light was the principal factor involved in photo-induced advances in sexual development and that the associated increases in feed intake played only a subsidiary role: whereas AFE in *ad libitum*-fed pullets was advanced by 33 d, those which had had their feed intake restricted to that of un-photostimulated controls reached sexual maturity within 4 d of the full-fed birds.

The enhanced nutrient intake stimulated by an increase in daylength also increases the rate of lipid deposition so that, despite an advance in sexual maturation, abdominal fat pads and total carcass lipid at first egg in photostimulated egg-type pullets are similar to those of later maturing, non-stimulated birds (Lewis and Perry, 1989*b*). The similarity of carcass fat content at first egg in the study, irrespective of AFE, and the well documented reduction in rate of fat deposition and delay in sexual maturation associated with restricted feeding (e.g., Lee, 1971) suggested a threshold of fat deposition for successful ovarian maturation. However, an investigation by Lewis and Perry (1992) confirmed, in modern hybrids, the findings of an earlier study (Morris, 1985) that accelerating fat deposition by feeding high energy diets does not advance maturity; it simply results in pullets having bigger fat deposits at puberty. This demonstrated that whereas nutritionally restricting growth and fat deposition during the rearing phase in egg-laying strains reduces the rate of sexual maturation (1 d per 1% reduction in body weight or 0.5 d per 1% feed restriction – Lee, 1971), nutritionally enhancing the processes does not accelerate it.

The nutritional control of growth has also been shown to strongly influence ovarian development in meat-type strains of pullets. Indeed, in the extreme, limiting the mean body

weight of dwarf broiler breeders to 1.0 kg completely prevented sexual maturation in both photostimulated and constant-photoperiod birds (Dunn and Sharp, 1992). Whilst the lack of photosexual response was probably due, in part, to an enforcement of photorefractoriness by the severity of the feed restriction, one of the principle reasons would most likely have been the suboptimal deposition of lipid. In most studies and in commercial practice, varying the degree of feed restriction only modifies gonadal development; it does not prevent it (Lewis *et al*., 2005*a,c*; Lewis and Gous, 2006*a,b*). Lewis (2006) concluded that mean ASM changes by about 2 d for each 100-g variation in mean body weight at 20 weeks (heavier birds maturing earlier). However, as observed in egg-type pullets, there appears to be an upper limit beyond which accelerated growth (and presumably faster rates of fat deposition and speedier dissipation of juvenile photorefractoriness) has no further interaction with the photosexual response; Lewis *et al*. (2007c) considered that allowing broiler breeders to have a mean body weight greater than 2.5 kg at photostimulation was unlikely to achieve any further advance in ASM.

2. CONSTANT PHOTOPERIODS

2.1 Constant photoperiods and sexual maturation in egg-type pullets

Original models

The effect of constant photoperiods on age at sexual maturity in *ad libitum*-fed egg-type pullets was originally reviewed by Morris (1967*a*) using data from 12 experiments (Ringrose, 1951, 1952; King, 1961, 1962; Siegel *et al*., 1961; McCluskey and Parker, 1963; Morris, 1966, 1967*a*, and unpublished from Reading University) that included treatments ranging from continuous darkness through to continuous illumination. A meta-analysis showed that the response could be described by a cubic regression, with the earliest maturity being achieved by giving pullets a constant photoperiod of between 16 and 17 h. The regression was described by the equation:

$$y = 170.2 - 1.610p + 0.00061p^2 + 0.001918p^3$$

where y = age at sexual maturity (d) and p = photoperiod (h).

The data were subsequently re-analysed by Lewis and Perry (pp. 362-363 in *World Animal Science: Poultry Production*, 1995), with the addition of four sets of data from trials conducted by the authors at Bristol University, to produce a new cubic regression. Differences among the data sets were removed by least squares; and the regression was described by the equation:

$$y = 154 - 3.44p + 0.206p^2 - 0.00376p^3$$

This equation predicted that the earliest maturity would be achieved by rearing on 13 h.

New models

Subsequently, Lewis *et al*. (1998*a*) noted that, in trials where there had been a 10-h treatment (King, 1961; Morris, 1967*a*; Lewis *et al*., 1996*d*), birds maintained on this photoperiod consistently matured earlier than any other photoperiod; thus questioning the appropriateness of the cubic regressions fitted by Morris (1967*a*) and Lewis and Perry

(1995). Whilst this observation suggested the use of two regressions, there was a problem in simultaneously removing differences among data sets with such analysis. The dilemma was resolved by the development of a new meta-analysis, termed a hinge analysis, by Curnow and Collins at the Department of Applied Statistics, University of Reading (details were presented in Lewis *et al*., 1998*a*). The new procedure was used to re-analyse the earlier data, together with additional data from Lewis *et al*. (1996*d*); and this showed that two opposing linear regressions were a significantly better fit (*P*<0.001) than a cubic regression, and identified a hinge point at 10 h (Figure 2.1). The regression equations were:

$$P \leq 10 \text{ h} \quad y = 175.8 - 1.731p \text{ (SE= 0.226)}$$

$$P \geq 10 \text{ h} \quad y = 155.5 + 0.304p \text{ (SE= 0.347)}$$

where *y* = mean age at first egg (d), *p* = constant photoperiod (h). However, the exactness of a 10-h photoperiod was probably a reflection of the data assembled, rather than any narrowly proscribed biological value, because there were 5 data points at 10 h and only one
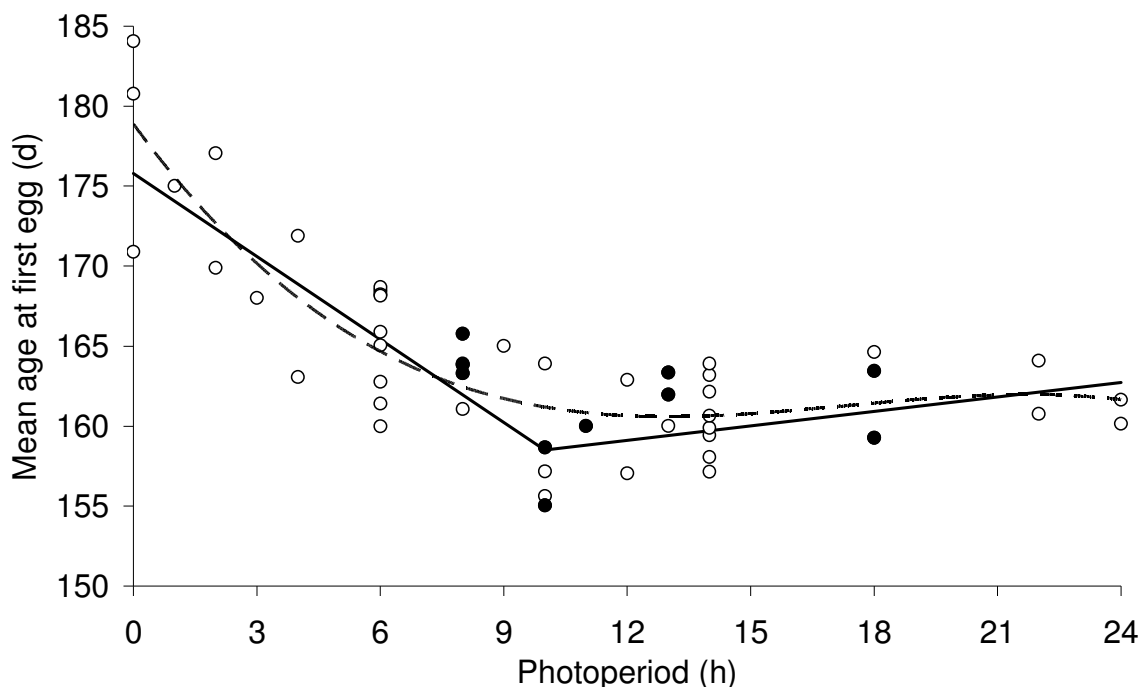

Figure 2.1 Regressions of age at first egg on constant photoperiod in early and modern genotypes of egg-type pullet (○ data from 12 data sets regressed by Morris (1967*a*), ● Lewis *et al*. (1996*d* and unpublished). The dotted cubic regression and solid red line hinged regression are from Lewis *et al*. (1998*a*).

point each at 9 h and 11 h, and so had 9.5 h been used in these trials instead of 10 h, the hinge point could well have been 9.5 h.

The significantly better fit of two regression lines over a cubic regression suggested that the photoperiodic influence on sexual development was not continuous but bimodal, with one component operating below the hinge and another above it. However, the non-significance deviation from zero of the rate of delay in maturation under photoperiods longer than 10 h reported by Lewis *et al*. (1998*a*) may suggest that photoperiod has only one effect; but one that operates only below the 10-h hinge. Although it has been shown that the feed intake of *ad libitum*-fed pullets during the prepubertal period is directly related to photoperiod (King, 1961; Morris, 1967*a*; Lewis *et al*., 2007*b*), and maturity is generally delayed by about 1 d for each 2% reduction in feed intake (Lee, 1971), Gous and Morris (2001) considered that the delay in sexual maturation which results from exposure to photoperiods shorter than 10 h is not a consequence of a reduction in feed intake but a response to photoperiod *per se* – an issue for further investigation

Subsequent to the publication of the model by Lewis *et al*. (1998*a*), it was apparent that the rates of delay in age at first egg for a 1-h reduction in photoperiod below 10 h in trials conducted since 1993 (Lewis *et al*., 1997*c*, 1998*a*, 2002 and unpublished; Gous and Morris, 2001) were markedly larger than for those conducted before 1967 and used by Morris (1967*a*) to produce the original model; and so data from the early trials were analysed separately from those of recent studies. These analyses showed that whereas there was no significant difference between modern and early hybrids in the hinge point or in the rate of response to daylengths longer than 10 h, modern hybrids had a significantly steeper response slope than early genotypes to photoperiods shorter than 10 h (Lewis and Morris, 2005). Indeed, despite modern hybrids maturing about 4 weeks sooner than early genotypes when reared on 10-h photoperiods, due principally to the intense genetic selection for egg numbers, the two types were predicted to have similar rates of maturation
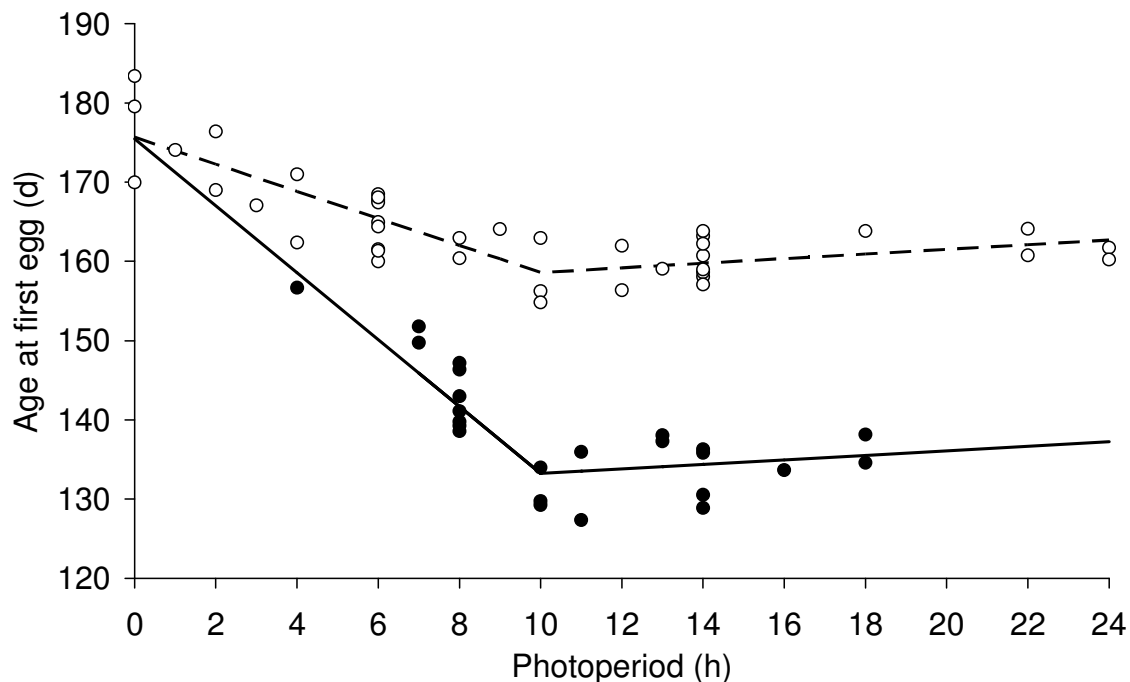
Figure 2.2 Regressions of age at first egg on constant photoperiod in early genotypes of egg-type pullet (○, broken line - published before 1967) and modern genotypes (●, solid - published after 1993 with dummy value of 173 d inserted at 0 h) from Lewis and Morris (2005).

when reared in complete darkness (Figure 2.2). Regressions for the two types of hybrid to photoperiods below and above the 10-h hinge were described by the following equations:

Early genotypes (12 data-sets, n = 40)		Modern genotypes (9 data-sets, n = 25)	
≤ 10 h	$y = 175.7 - 1.707p$	≤ 10 h	$y = 175.5 - 4.222p$
≥ 10 h	$y = 155.6 + 0.294p$	≥ 10 h	$y = 130.4 + 0.285p$
(P< 0.001, residual SD = 4.53)		(P< 0.001, residual SD = 4.56)	

where y = mean age at first egg (d), and p = constant photoperiod (h).

2.2 Constant photoperiods and sexual maturation in broiler breeders

There were no reports in the literature for the comparative effects of constant daylengths on sexual maturation in female broiler breeders. A meta-analysis of data from Lewis *et al.* (2003*a*, 2004*a*, 2007*c*) and from Renden *et al.* (1991) for initial semen production in males showed both similarities and differences between broiler breeder and egg-type strains (Figure 2.3). Figure 2.2 showed that the responses of egg-laying birds to < 10-h days had changed in response to the intense selection for egg numbers, and so, because selection for
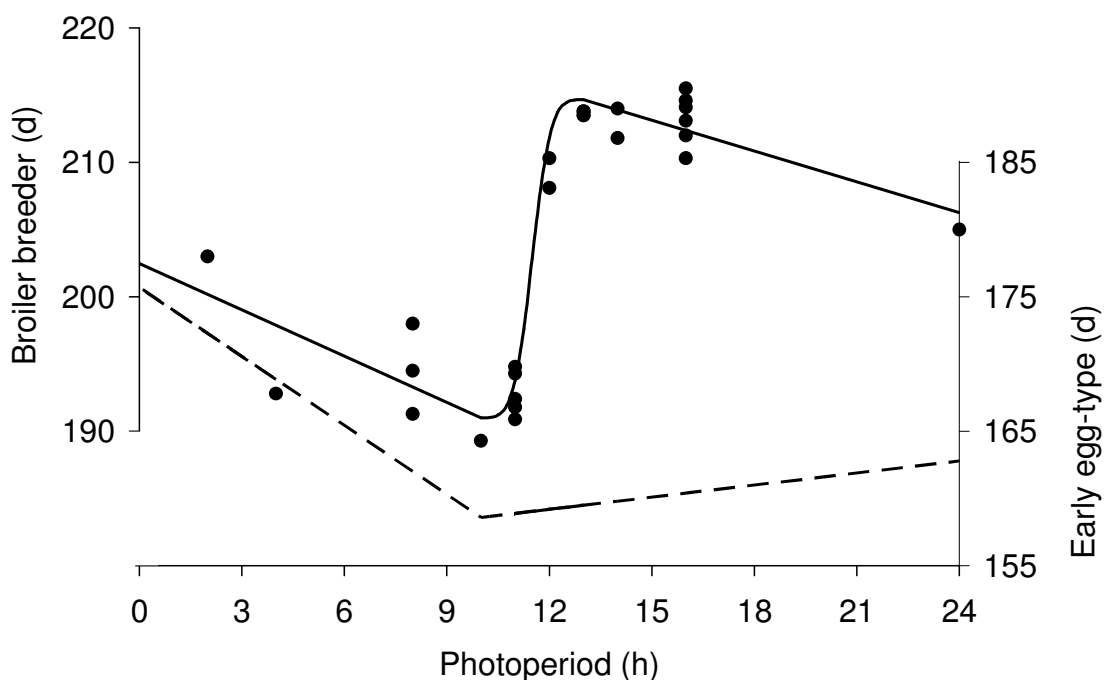
Figure 2.3 A comparison of the effect of constant photoperiod on sexual maturation in broiler breeders (solid line) and early strains of egg-type pullet (broken line) (Lewis, 2006).

egg numbers has been minimal in broiler breeders, their response was compared with early strains of egg-laying hybrid. The progressive advance in sexual maturity, as photoperiod increases to 10 h, and the inducement of the earliest AFE by a 10-h photoperiod are similar for the two types of stock. However, for photoperiods between 10 and 24 h, the response of broiler breeders is very different from egg-laying hybrids. Whereas photoperiods > 10 h result in a slight, but progressive delay in AFE in egg-type strains; there is a significant delay of 3 to 4 weeks between 10 and 13 h in broiler breeders, but a gradual advance in maturation beyond 14 h. The marked disparity in rate of sexual development between 10 and 13 h is most probably a reflection of the differences in stimulatory competence among these photoperiods and in the degree to which they facilitate the dissipation of photorefractoriness. Indeed, the significantly later maturity of pullets reared on long days compared with short days provided important evidence for the conclusion that broiler breeders exhibit photorefractoriness (Lewis *et al.*, 2003*a*).
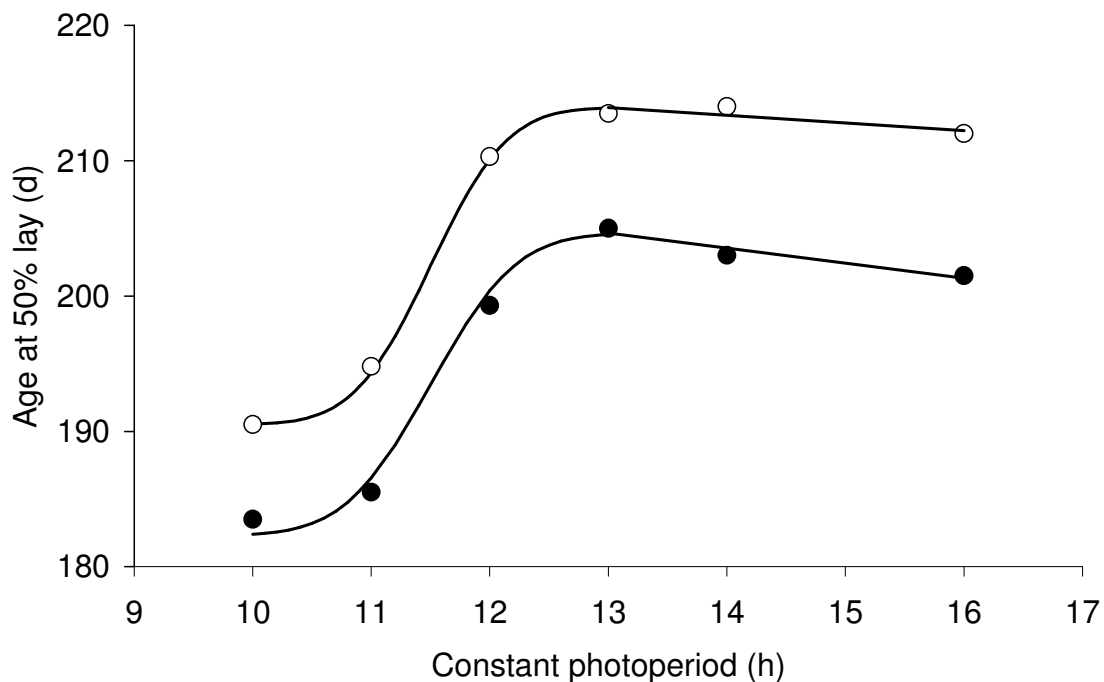
Figure 2.4 Age at 50% rate of lay in broiler breeders grown to reach 2.1 kg body weight at 17 weeks (○) or 21 weeks of age (●) and maintained on 10-, 11-, 12-, 13-, 14- or 16-h photoperiods (Lewis *et al.*, 2004a).

Although growth rate exerts a large influence on the rate of sexual maturation in meat-type pullets (± 2 d for each 100-g change in 20-week body weight - Lewis, 2006), it only alters the amplitude and not the relative response of broiler breeders reared on a constant photoperiod (Lewis *et al.*, 2004*a*) (Figure 2.4).

2.3 Constant photoperiods and laying performance in egg-laying hens

Commercial laying hens are rarely given constant photoperiods, and so the following responses are of biological interest only. Data presented by the author to the *XXth World Poultry Congress* in 1996 indicated that when laying hens, be they white- or brown-egg hybrids, are kept on a constant photoperiod, egg production to 72 weeks of age increases by about 4 eggs per 1 h of photoperiod up to about 10 h, but that the response appears to be genotype-dependent beyond 10 h. Data from McCluskey and Parker (1963), Morris (1979),
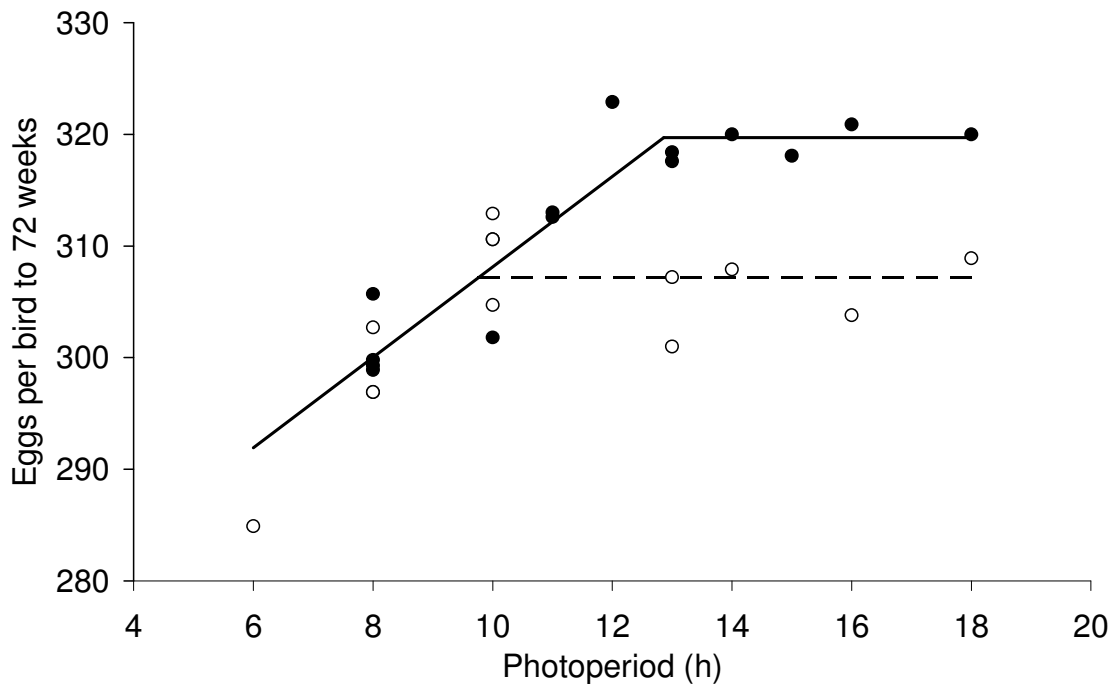
Figure 2.5 Effect of constant or laying-phase photoperiod on egg numbers to 72 weeks in white-egg (○, broken line > 10 h) and brown-egg (●, solid line) hybrids (Lewis, 1996).

and trials conducted by the author at the University of Bristol suggested that egg production plateaus, and may even decline, when white-egg hybrids are given a daylength longer than 10 h, whilst other Bristol data and reports from Morris *et al*. (1995) indicated that mean rate of lay in brown-egg hybrids continues to increase with extensions of photoperiod up to about 13 or 14 h (Figure 2.5).

Mean egg weight (MEW) to 72 weeks of age increases by 0.1-0.2 g per 1 h of photoperiod, though the rate of increase is greater in white-egg than in brown-egg hybrids; probably an artefact of the plateauing of rate of lay by white-egg genotypes beyond 10 h (*XXth World Poultry Congress:* Lewis, 1996).

2.4 Constant photoperiods and laying performance in broiler breeder hens

Commercially, broiler breeders are unlikely to experience constant photoperiods unless they are kept in open-sided, non-illuminated housing close to the equator. Thus the

following descriptions of their biological responses to photoperiod are, in the main, of academic interest only.

The number of eggs laid to 60 weeks (normal depletion age for broiler breeders) is strongly influenced by ASM and, because ASM is not linearly related to photoperiod, the relationship of egg production with photoperiod is also non-linear. The earliest sexual development occurs in birds exposed to 10-h photoperiods (Figure 2.3), and so birds maintained on 10 h also lay most eggs. Egg production falls by about 8 eggs for each 1-h shorter photoperiod below the 10-h hinge and by 3-4 eggs for each 1-h increase above the hinge (Lewis *et al*., 2005*a*). Reproduction terminates in most seasonal-breeding avian species after prolonged exposure to stimulatory daylengths because of the onset of adult photorefractoriness. The same phenomenon occurs to a lesser extent in broiler breeders and is one of the causes of the more rapid decline in rate of lay after peak production in broiler breeders compared with egg-laying hybrids (Lewis *et al*., 2003*a*).

Mean egg weight in broiler breeders is correlated with age and body weight at first egg (Lewis *et al*., 2005*a*), but, as in egg-laying hybrids (Lewis *et al*., 1994*c*), a multiple regression of MEW on ASM, body weight at sexual maturity (BWSM), and photoperiod (*p*) shows that MEW still varies with photoperiod even when the effects of ASM and BWSM are removed:

$$MEW = 53.8 + 2.30BWSM + 0.04ASM + 0.10p$$

Although this revealed a significant linear effect of photoperiod, further analysis of the data following adjustment to a 202-d ASM and 3.50-kg BWSM suggested that a bent-stick model would be a better fit. Such a model indicated that MEW increased by about 1 g per 1 h of photoperiod up to a constant daylength of about 13 h, but levelled out thereafter (Figure 2.6). This contrasts with the continued photoperiodic effect on MEW reported for egg-laying hybrids (*XXth World Poultry Congress:* Lewis, 1996). However, egg-type hybrids are fed *ad libitum*, which allows them to continue to increase feed intake on longer
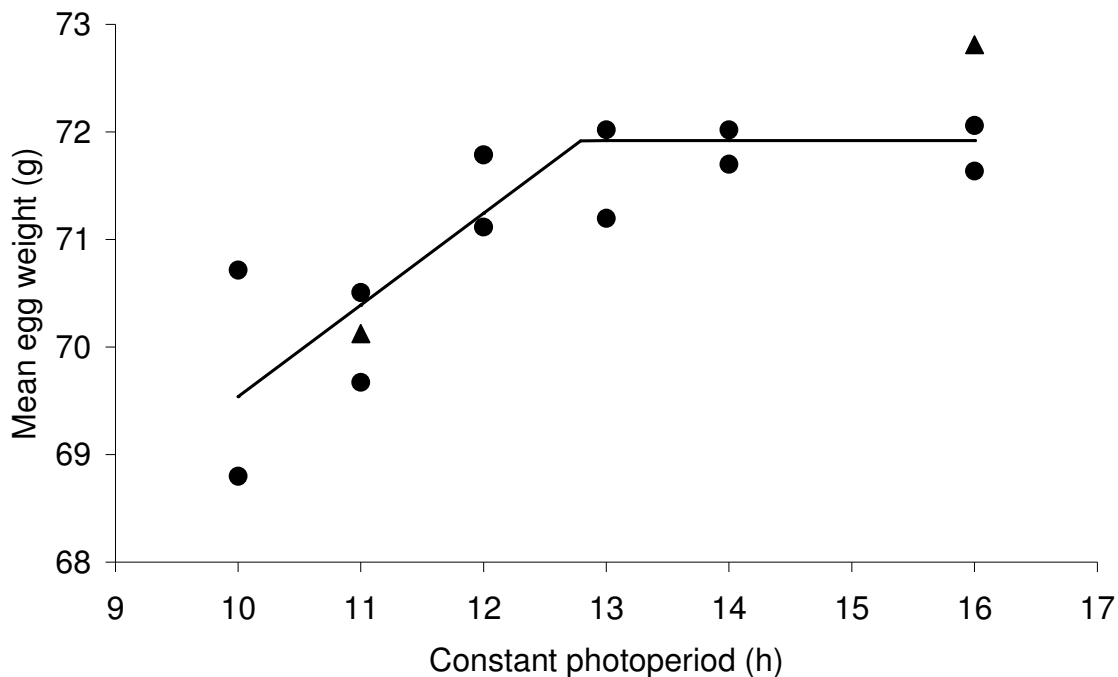
Figure 2.6 Mean egg weight to 60 weeks of age for broiler breeders maintained on various constant photoperiods from 2 d of age (▲ Lewis *et al*., 2003*a*; ● Lewis *et al*., 2005*a*). Data adjusted to a mean ASM of 202 d and mean body weight at sexual maturity of 3.5 kg with differences between trials removed by least squares analysis.

photoperiods and to use the extra nutrients to increase MEW; an option not available to broiler breeders given fixed daily allocations of feed.

Lighting history does not appear to interact with the effect that prevailing daylength has on shell thickness and shell weight in domestic hens, and so the data reported by Backhouse *et al*. (2005) for broiler breeders maintained on constant photoperiods from soon after hatch will be equally applicable to birds given a conventional step-up lighting regimen. Shell weight and thickness index (mg/cm²) are both negatively correlated with photoperiod, with weight decreasing by 30 mg and thickness index by 0.57 mg/cm² for each 1-h extension of the photoperiod; these are similar deterioration rates to those reported for egg-laying hybrids (Lewis *et al*., 1994*d*).

3. CHANGING PHOTOPERIODS

3.1 Changing photoperiods and sexual maturation in egg-type pullets

Original models

It has long been known that changes in photoperiod have a greater effect on sexual maturation than photoperiod *per se* (e.g., Whetham, 1933). Morris and Fox (1958*a*) observed that increases in daylength advance maturity and decreases retard it, and concluded that sexual maturity in naturally illuminated pullets could be predicted by the net change in daylength experienced during the rearing period according to the equation:

$$y = m \pm 1.64 \, \Delta D$$

where y = age at first egg (d), m = mean age at first egg for a given genotype when reared on a constant photoperiod (d), and ΔD is the net change in photoperiod (h). However, Morris (1962) considered that the model made several incorrect assumptions: equal amounts of increase and decrease in daylength would cancel each other, pullets were equally photosensitive at all ages, the actual initial and final photoperiods were unimportant, and the 1.64 coefficient was applicable to all genotypes. Morris used data from studies conducted at Reading University and from Bowman and Jones (1963) to suggest that a pullet gradually became more sensitive to a change in photoperiod with age, at least up to 15 weeks. However, the treatments invariably involved only decreases, rarely increases, in photoperiod, and so the conclusion was not a general age-related response to change in photoperiod. Morris (1962) demonstrated that the initial and final photoperiod was more important than the actual change in photoperiod, and suggested that the maximum influence on maturity was achieved by making changes close to 12 h, but there were insufficient data available to construct a satisfactory response curve. Morris also concluded that, despite having a satisfactory general explanation for the effects of constant

and changing photoperiod on sexual maturation, any prediction equations would be too complicated and unreliable to be of practical value.

New model

Reports in the literature for the influence of age at photostimulation on AFE in egg-type pullets published prior to the model of Lewis *et al*. (2002) included neither treatments young enough to produce other than linear regressions (Figure 3.1) nor transfers from photoperiods other than 8 h. And so a series of studies were conducted to determine the responses to photoperiodic increments given before 14 weeks and from different initial photoperiods (Lewis *et al*., 1996*b*,*d*, 1997*b*, 1999*b*, 2002). Findings from these trials enabled the construction of a model to predict mean AFE in pullets given a single increase in photoperiod; this involved five distinct phases (Lewis *et al*., 2002) (Figure 3.1):

- A period of about 5 weeks in which the hypothalamo-pituitary-gonadal axis is maturing, and in which no birds are responsive to an increase in photoperiod.

- A period between 5 and 9 weeks when there is a bimodal distribution of birds: some photosensitive and able to respond to the increment by accelerating their gonadal development; and others still not photoresponsive and maturing as if maintained on the initial photoperiod. Mean AFE in this phase depends on the proportion of birds within each category.

- A period from about 9 weeks of age in which the response to the increment is linear, but progressively reducing until the first bird spontaneously starts rapid ovarian development in response to the initial photoperiod.

- A phase in which some birds mature spontaneously before the photoperiod is increased, whilst others continue to have their gonadal development accelerated by the increment.

- A final phase in which all birds commence rapid gonadal development before the increment is given and therefore non-responsive when the increase occurs.
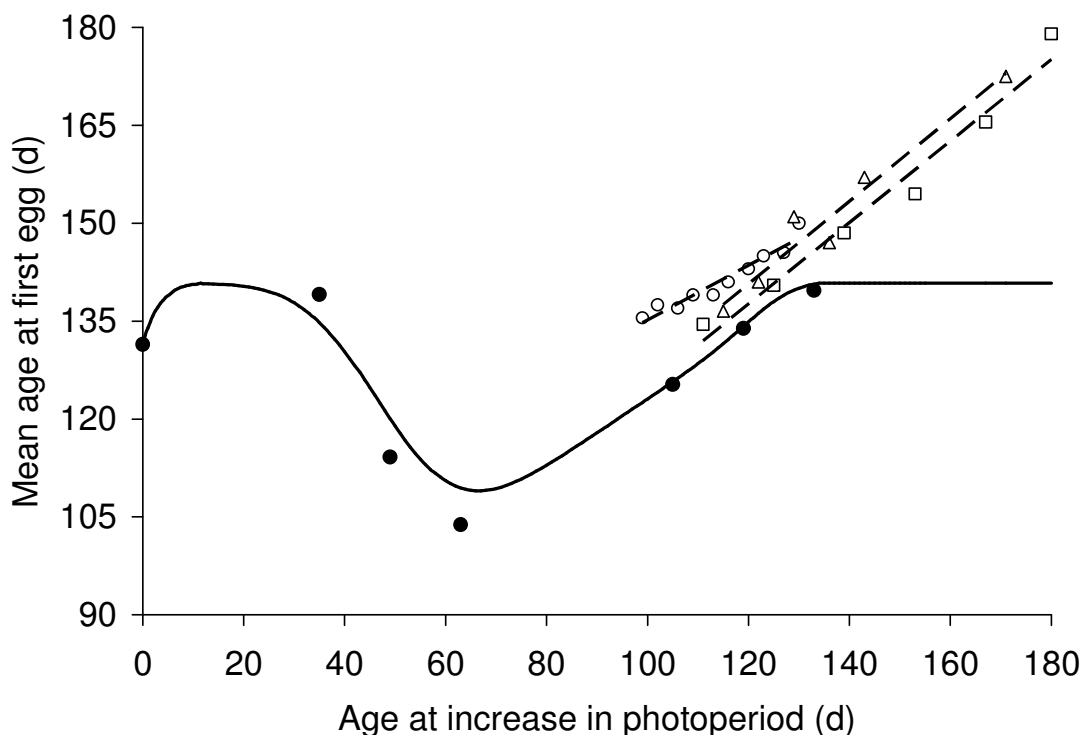
Figure 3.1 Model for the effect on mean age at first egg of age at transfer from 8 to 16 h in ISA Brown hybrids, with data (●) from Lewis *et al.* (2002). Unadjusted data with linear regressions for other genotypes: (○) Leeson *et al.* (1988), (□, △) Gous *et al.* (2000).

There had been many studies of the age-related influence of a decrease in photoperiod on sexual maturation in pullets (e.g., Bowman *et al.*, 1964; Morris, 1966), and all had demonstrated the retarding effect on sexual development. However, most used transfers between very long and very short photoperiods (e.g., 18 or 22 h to 6 h), and Morris (1962) had already suggested that the maximum influence on maturity would be achieved by making changes close to 12 h. Accordingly, more trials were conducted to measure the effect of changes to and from more stimulatory photoperiods (Lewis *et al.*, 1996*d*, 1998*d*, 2002), and to determine the effect of initial and final photoperiod (Lewis *et al.*, 1996*d*). The findings of these and earlier studies allowed the construction of a model to predict mean AFE in pullets given a single decrease in photoperiod (Figure 3.2). Responses to a decrease in photoperiod are less complex than to an increase because pullets are responsive
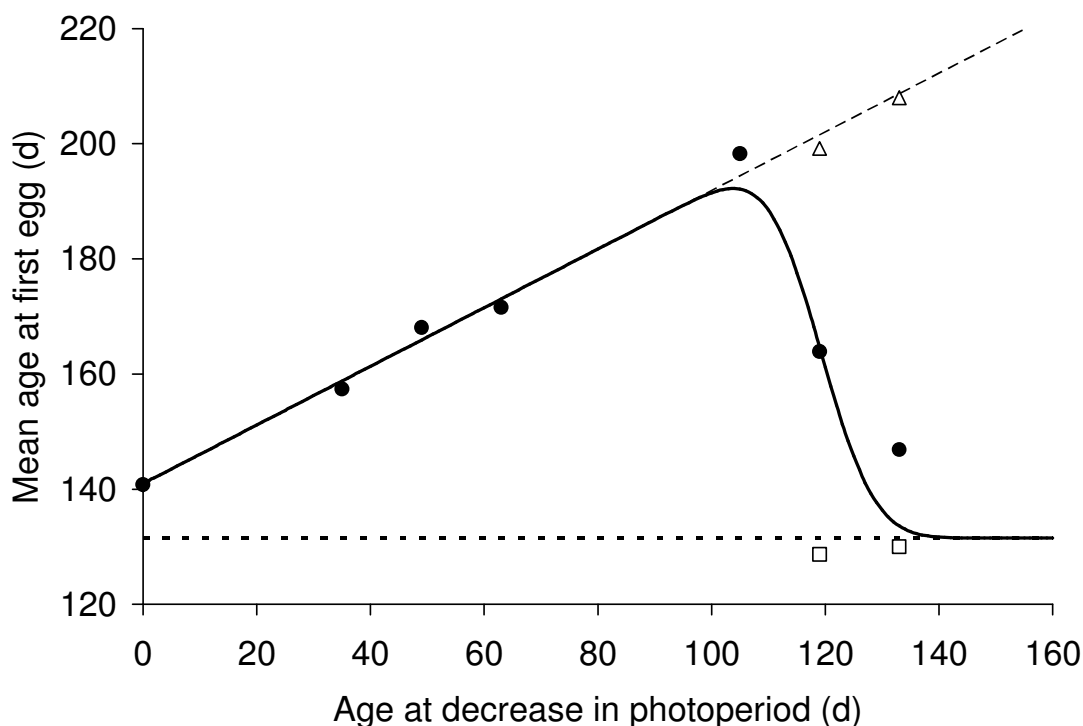
Figure 3.2 Model for the effect on mean age at first egg of age at transfer from 16 to 8 h in ISA Brown hybrids, (●, solid line) mean of all birds, (Δ, broken line) mean of responding birds, (□) mean of birds maturing spontaneously in response exposure to a constant 16-h photoperiod, and (horizontal dotted line) constant 16-h (Lewis *et al*., 2002).

from day old and do not require a period in which to acquire sensitivity. This means that there are only three phases in the response to a decrease in daylength:

- A period between hatch and the first bird spontaneously starts rapid ovarian development in response to the initial photoperiod, and in which birds become progressively more sensitive to a decrease.

- A phase in which some birds mature spontaneously before the photoperiod is reduced, whilst others continue to have their gonadal development retarded by a decrease.

- A final phase in which all birds commence rapid ovarian and oviducal development before the photoperiod is decreased, and are therefore no longer responsive to a change in photoperiod.
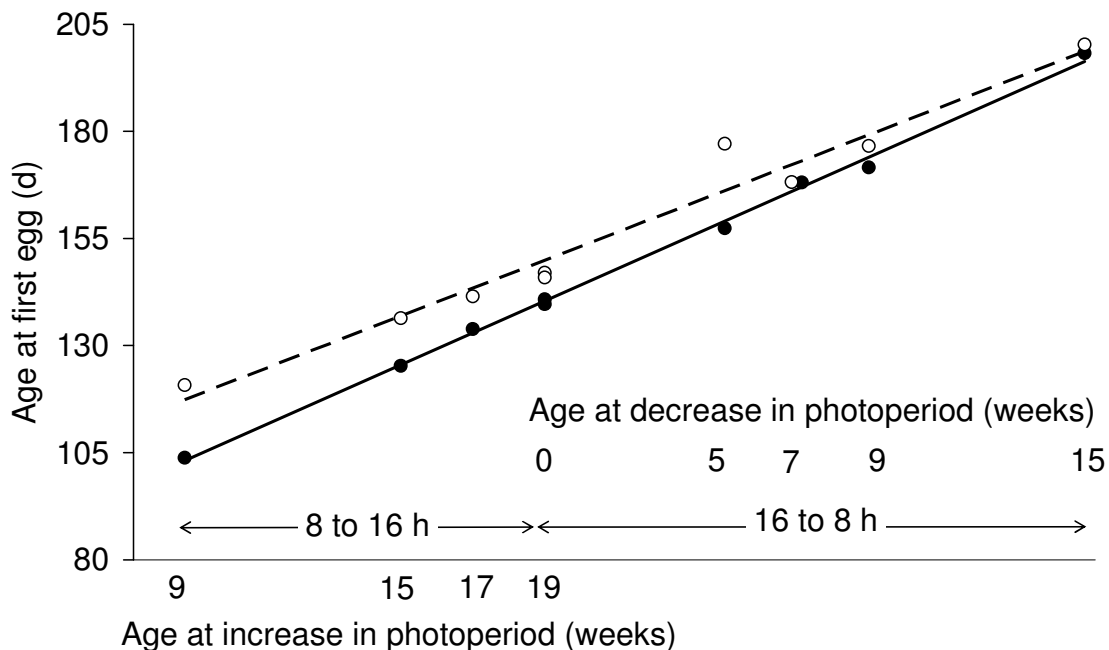
Figure 3.3 Effect of age at transfer from 8 to 16 h (left side of graph) or from 16 to 8 h (right side of graph) on sexual maturation in (●) ISA Brown hybrids and (○) Shaver 288 hybrids (Lewis *et al.*, 2002).

An amalgamation of the responses to changes from 8 to 16 h with those for changes from 16 to 8 h for brown-egg (ISA Brown) and white-egg (Shaver 288) hybrids (Lewis *et al.*, 2002) indicated that the rate of change in mean AFE (*b* value) for a given change in age at which changes were given were similar (Figure 3.3). These and earlier data were used to produce an equation that predicts the rate of response by ISA Brown pullets to a change between any pair of photoperiods (Figure 3.4). The linear regressions for the two genotypes in Figure 3.3, though having different slopes, suggested that provided there is information for a given change (increase or decrease) in daylength applied at two or more ages, a response, relative to ISA Brown, can be predicted for any genotype by calculating an adjustment factor (*k*). The original equation was subsequently amended to give a better estimate of *b* for extreme changes in photoperiod by Lewis and Morris (2004):

$$b = k_i(0.1338 + 0.1496C - 0.01884C^2 + 0.0009683C^3 - 0.00001941C^4 - 0.22396M$$

$$+ 0.05028M^2 - 0.00365M^3 + 0.00008216M^4$$

where C = change in photoperiod (h) and M = mean photoperiod (h).
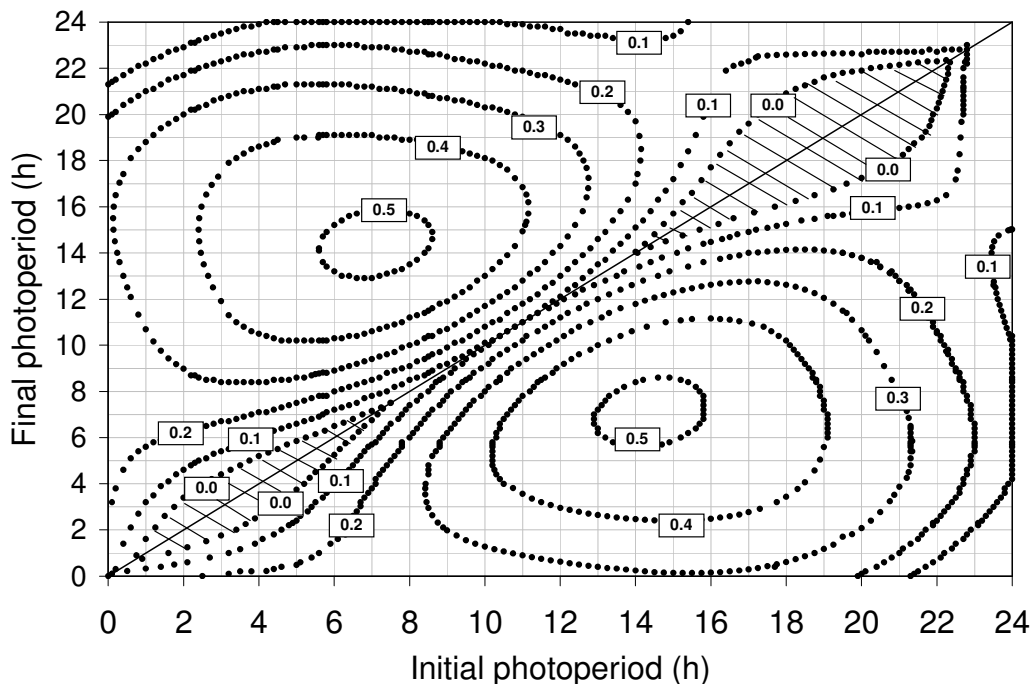
Figure 3.4 Effect of initial and final photoperiod on rate of change in mean AFE for a delay in change in photoperiod (*b* value) for ISA Brown hybrids (Lewis and Morris, 2004).

Effect of genetic selection on age at sexual maturity

Eleven studies of responses to an increase in photoperiod given at about 9 weeks (when a pullet is most photosensitive) or 17 weeks of age (when it is approaching spontaneous rapid gonadal development) were conducted at the University of Bristol by the author between 1987 and 1999. Analyses of these data (Figure 3.5) showed that the modern egg-laying hybrid, as typified by the ISA Brown, had become less responsive to an increment given late in the rearing period due, most likely, to the genetic advance in sexual maturity (Lewis *et al.* 2000*b*). The slopes of regressions of mean AFE for birds maintained on 8 h on the year in which their originating grandparent flock had been hatched (-0.87 d/year) and for those transferred to a stimulatory photoperiod at about 17 weeks (-0.68 d/year) were not significantly different. In comparison, the slope of the regression for pullets photostimulated at 17 weeks was, at -1.49 d/year, significantly steeper. The difference in slope between birds transferred to a stimulatory photoperiod at 9 and 17 weeks indicated
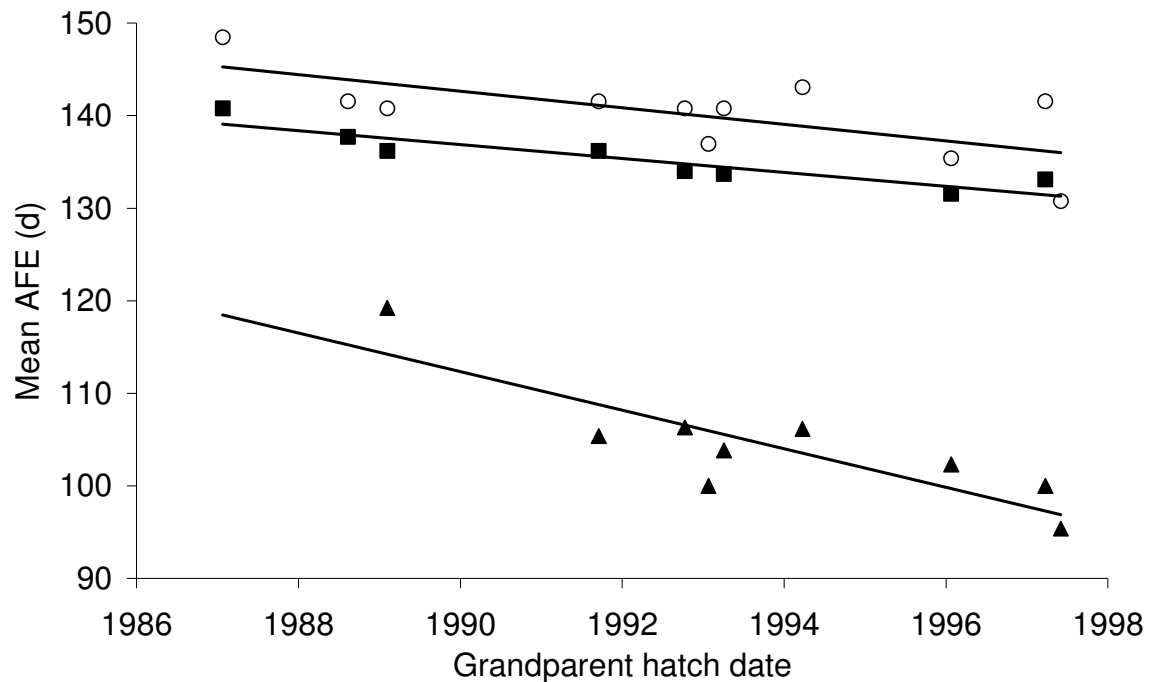
Figure 3.5 Regressions of mean age at first egg on grandparent hatch date for the same strain of brown-egg hybrid maintained on 8-h photoperiods (○), or transferred to a stimulatory photoperiod at 9 (▲) or 17 (■) weeks of age (Lewis *et al*., 2000*b*).

that pullets became less responsive to a photoperiodic increment given late in the rearing period and more responsive to one given close to peak photosensitivity as the rate of sexual maturation increased (undoubtedly, a consequence of the intense genetic selection for egg numbers). Notwithstanding that all three regressions were significantly linear, physiological limits to rapid gonadal development dictate that the rate of advance in AFE cannot continue indefinitely at these rates.

3.2 Changing photoperiods and sexual maturation in broiler breeders

Previous studies of the effect of age at photostimulation on AFE in broiler breeders, e.g., Robinson *et al.* (1996) and Joseph *et al.* (2002), had the same limitations as the early photoperiodic studies in egg-type birds, where transfers to long days were made too late to demonstrate responses prior to the acquisition of photosensitivity and too early to detect when the last bird commenced sexual development in response to the initial photoperiod.
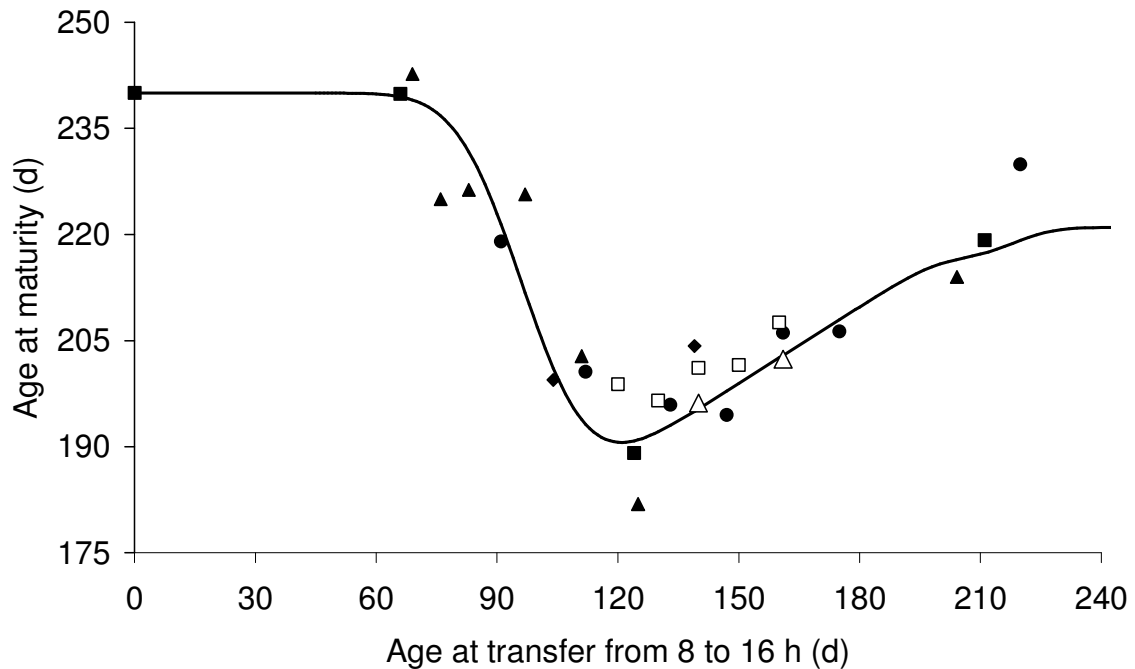
Figure 3.6 Mean age at sexual maturity for broiler breeders weighing about 2.1-kg body weight at 20 weeks of age and transferred at various ages from 8- to 16-h photoperiods: Lewis *et al.*, 2003*a* (■), Lewis *et al.*, 2007*c* (●), Ciacciariello and Gous, 2005 (♦,▲), Robinson *et al.*, 1996 (□), Joseph *et al.*, 2002 (Δ).

Prior to the research at the University of KwaZulu-Natal, there were insufficient data for the influence of initial and final photoperiods, the interacting effect of growth with lighting, or the involvement of photorefractoriness in broiler breeder photoperiodism to construct a model similar to that produced by Lewis *et al.* (2002) for egg-laying strains. A series of trials was therefore conducted to fill these gaps in our knowledge (Ciacciariello and Gous, 2005; Lewis and Gous, 2006*b,c,d*, 2007*b*; Lewis *et al.*, 2003*a*, 2005*b*, 2007*c*).

Figure 3.6 shows that although the general profile of the broiler-breeder response to an increase in photoperiod is similar to that for egg-type genotypes (Figure 3.1), there are fundamental differences in the ages at which the five phases of the model occur and in the relative influences of initial and final photoperiod on sexual maturation. Findings from trials in which the same lighting treatments were applied to birds with different growth profiles (Ciacciariello and Gous, 2005; Lewis and Gous, 2006*a,b*; Lewis *et al.*, 2005*b*, 2007*c*) indicated that body weight can have a large influence on the rate at which a broiler
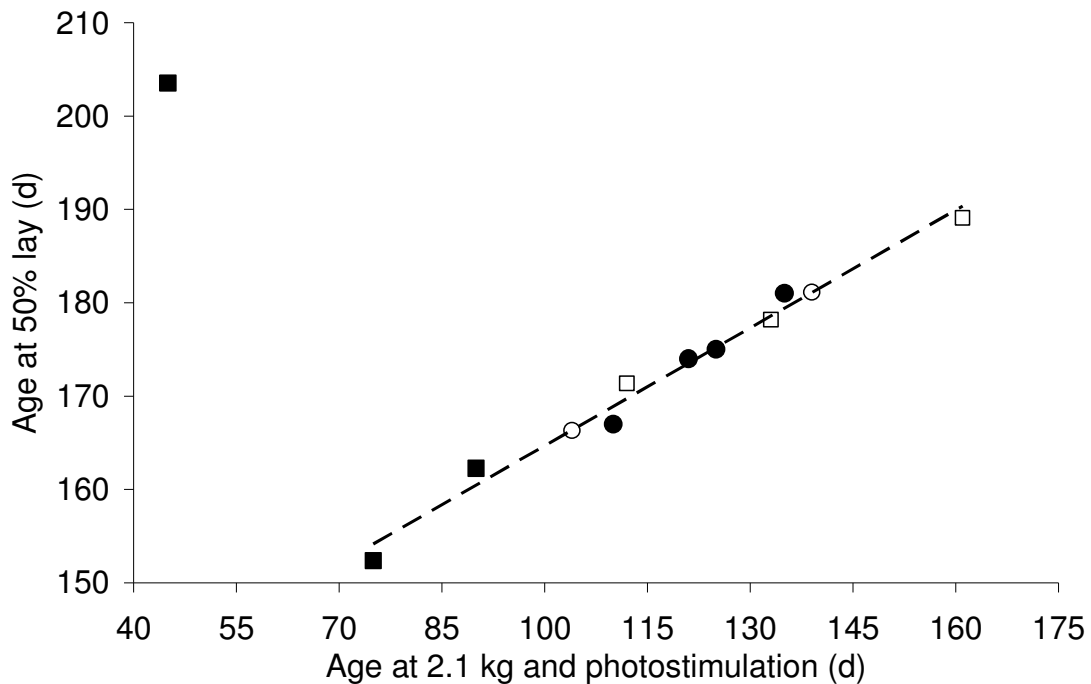
Figure 3.7 Mean age at 50% egg production for broiler breeders transferred from 8 h to a stimulatory photoperiod (11, 12, 14 or 16 h) at various ages but at approximately 2.1 kg body weight (● Leeson and Summers, 1983; ○ Ciacciariello and Gous, 2005; ■, □ Lewis *et al.*, 2007*c*). Differences among trials were removed by least squares analysis.

breeder dissipates photorefractoriness and in the subsequent response to an increment in photoperiod. Lewis (2006) concluded that the effect of body weight for birds given a change in photoperiod was, at ± 2 d for each 100-g change in 20-week body weight, similar to that for birds given constant daylengths (Figure 2.4). However, photostimulating birds at different ages when they have been grown to different growth profiles generally means that they have been transferred to long days at different body weights, thus confounding body weight and age. Lewis (2006) separated the two factors by performing a meta-analysis of data from studies in which normal broiler breeders had been photostimulated at different ages but at the same mean body weight (2.1 kg) (Leeson and Summers, 1983; Ciacciariello and Gous, 2005; Lewis *et al.*, 2007*c*). Data in Figure 3.7 show that, for birds weighing 2.1 kg and aged between 75 and 161 d of age, sexual maturity advances by about 4 d for each 10-d younger age at which they are

photostimulated. The markedly later maturity of birds fed *ad libitum* and weighing 2.1 kg at 45 d indicates that, even when body weight is not limiting, more than 45 short days are required to dissipate juvenile photorefractoriness.

An increment in photoperiod given at about 20 weeks of age to broiler breeders reared on 8-h photoperiods and weighing about 2.1 kg accelerates gonadal development, but the size of the advance in ASM depends on the photoperiod to which the birds are transferred. Prior to the availability of the findings shown in Figure 1.5, a meta-analysis of data from three studies conducted at the University of KwaZulu-Natal in which birds were reared on 8-h day showed a curvilinear relationship between mean ASM and final photoperiod, with the earliest maturity being induced by a transfer to between 14 and 16 h (Lewis, 2006). The relationship between final photoperiod (*p,* h) and ASM (d) was described by the equation:

$$ASM = 288.2 - 13.54p + 0.463p^2$$
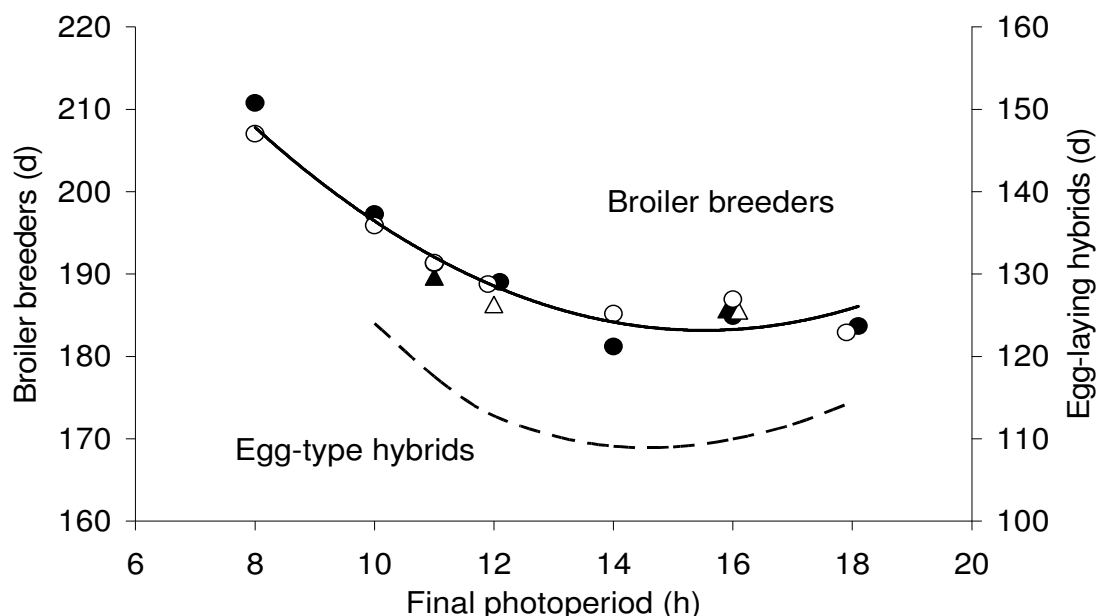
Figure 3.8 Mean age at 50% lay for broiler breeders weighing 2.1 kg and transferred at 140 d from 8 h to various final photoperiods (▲ Lewis *et al*., 2003*a*; △ Ciacciariello and Gous, 2005; ●,○ Lewis and Gous, 2006*b*). The broken line shows the predicted response of egg-laying pullets photostimulated at the same physiological age (70 d) (Lewis *et al*., 2002; Lewis and Morris, 2004).

Predicted mean ASM for *ad libitum*-fed egg-type hybrids photostimulated at 10 weeks (equivalent to 'physiological age' of a 20-week control-fed broiler breeder) using the models of Lewis *et al*. (2002) and Lewis and Morris (2004) show that egg-laying pullets and broiler breeders respond similarly to final photoperiod when reared on 8-h days (Figure 3.8).

There had been no earlier studies of the effect of photoperiod during the rearing phase on ASM in broiler breeders prior to that of Lewis and Gous (2006*c*). However, there was only one transfer-age (140 d) and only one final photoperiod (16 h) used in this study, and so it provided insufficient data to construct a contour chart of *b* values similar to that published by Lewis and Morris (2004) for egg-type strains (Figure 3.4). Nevertheless, because of the similarity of the responses of the two types of stock to final photoperiod (Figure 3.8), Lewis *et al*. (2007*g*) suggested that the egg-type pullet equation (p. 38) could be used for broiler breeders with a suitable *k* value. The *k* values were calculated by dividing the *b* values for broiler breeders (estimated by using the equation on p. 43) by the *b* values for egg-type pullets. However, it was apparent that a common *k* value could not be used for all photoperiods, and subsequent analysis showed that *k* could be estimated from the final photoperiod (*p,* h) using:

$$k = -0.449 + 0.155p - 0.00547p^2$$

Lewis and Gous (2006*c*) concluded that ASM in birds reared from soon after hatch on 6-, 8-, or 10-h photoperiods and transferred to 16 h at 140 d were not significantly different. The similarity was a consequence of the slightly slower sexual development of the birds reared on an 6- or 8-h photoperiod, relative to a 10-h (Figure 2.3), being countered by the larger, more stimulatory increment in photoperiod given to them at 140 d. This does not mean that daylength during the rearing period is unimportant, but that 6-, 8- and 10-h daylengths are short days and so all groups will have been photosensitive when they were transferred to 16 h at 140 d. The situation is very different when broiler breeders are reared

on longer daylengths because the acquisition of photosensitivity is delayed and the birds have a reduced or no opportunity to be photostimulated (Gous and Cherry, 2004; Lewis and Gous, 2006*c*).

The model to estimate ASM in broiler breeders given a single increment in daylength (Lewis *et al*., 2007*g*) contains the same five components as the model produced by Lewis *et al*. (2002) for egg-laying genotypes, but with appropriate adjustments for differences in 20-week body weight (Figure 3.9).

Practical application of the broiler breeder model

In commercial practice, broiler breeders are usually given a series of increments and not a single change in photoperiod, but there is no significant difference between the two regimens in either sexual maturity or subsequent laying performance (Lewis and Gous, 2006*d*), and so use of the model is perfectly appropriate for predicting ASM in most flocks of broiler breeders.

3.3 Late increments in photoperiod for broiler breeders

It had previously been suggested that the ideal way to light broiler breeders was to initially transfer them to a photoperiod somewhere between the critical and saturation photoperiods for LH release, and not to give further increments until they were required to balance the progressive decline in LH release associated with the development of adult photorefractoriness (Sharp, 1993). However, two studies conducted at the University of KwaZulu-Natal showed that broiler breeders do not respond positively to photoperiodic increments given during the laying phase. Indeed, irrespective of the size and timing of the increments, extending the daylength to 16 h after an initial increase to 11 h at 140 d of age only serves to accelerate the decline in rate of lay, most likely through an advance in the onset of adult photorefractoriness (Lewis *et al*., 2007*f*).
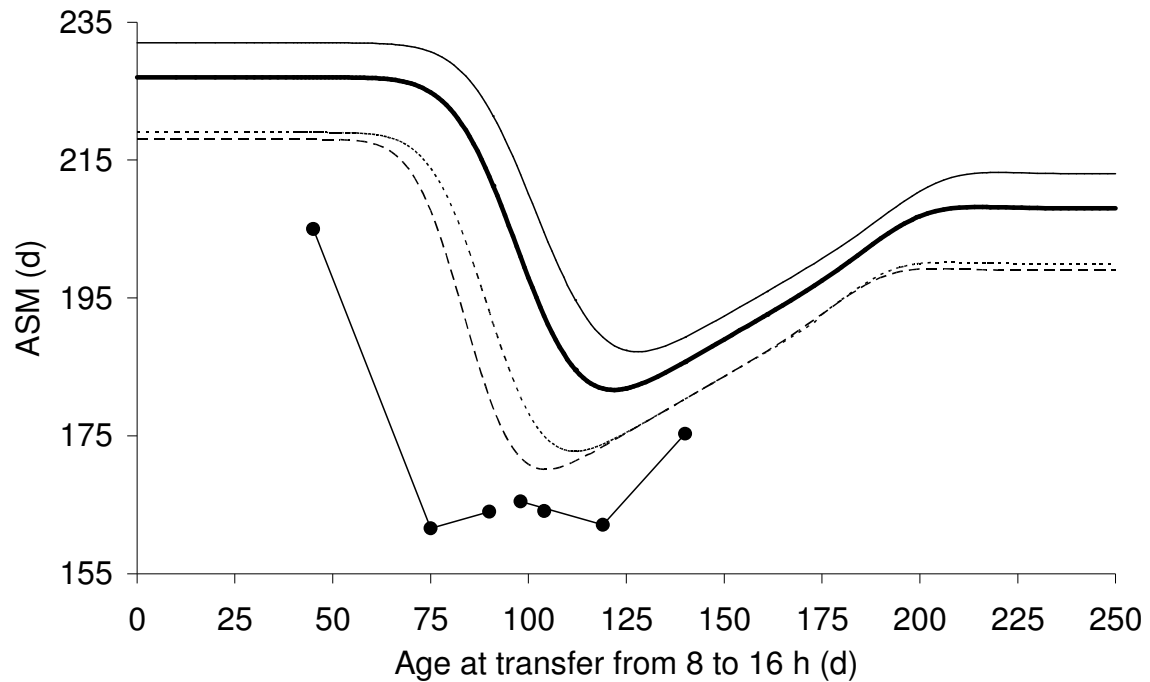
Figure 3.9 Models for the effect of age at photostimulation on mean ASM for broiler breeders grown to a mean 20-week body weight of 1.85 kg (thin solid line), 2.1 kg (thick solid line), 2.5 kg (dotted line), or 2.8 kg (broken line). Raw data (●) are presented for birds with a 20-week body weight of ≥ 3.13 kg (Lewis *et al.*, 2007*g*).

Influence of growth on the response of broiler breeders to an increase in photoperiod

Although providing a constant photoperiod to groups of broiler breeders with different mean body weights alters the amplitude but not the shape of the response to photoperiod (Figure 2.4), the response to a transfer from short to long days is extensively affected by both age and body weight at photostimulation (Figure 3.9). This is because the rate at which a bird dissipates juvenile photorefractoriness is strongly influenced by its rate of growth, and this will have an immense effect on its response to a change in photoperiod. For example, broiler breeders grown to a 20-week body weight of 2.8kg matured 12 d earlier than birds weighing 2.1 kg when transferred from 8 to 16 h at 125 d, but 41, 24, 11, 64 and 25 d earlier when the transfer to long days was made at 69, 76, 83, 97 and 111 d respectively (Lewis *et al.*, 2007*c*).

3.4 Relevance of research findings to the broiler breeder industry

There was a dearth of information on the broiler breeder's response to lighting prior to the research conducted at the University of KwaZulu-Natal, with most lighting programmes being based on our knowledge of lighting *ad libitum*-fed egg-laying breeds. However the subsequent demonstration of photorefractoriness in broiler breeders showed that some aspects of their lighting strategy, such as that to rear spring-hatched birds on a photoperiod equal to the anticipated longest natural daylength when they are reared in non-lightproof facilities, have been incorrect. Whereas the aim of the long-day rearing strategy in egg-type pullets was to minimise precocity, the incidence of prolapse, and the production of small eggs, this policy was misplaced in broiler breeders because their sexual maturation is largely under controlled by the feeding programme, and the consequences of not rearing on a short daylength is a delay in the acquisition of photosensitivity, a significant delay in gonadal development, and a reduction in egg numbers (Lewis and Gous, 2006*c*, 2007*b*; Lewis *et al.*, 2005*b*).

3.5 Comparisons of domestic fowl '*b*' values with other avian species

A comparative analysis by Lewis and Morris (1998*b*) of data from literature and studies conducted by the author at the University of Bristol for the effect of age at transfer to a stimulatory photoperiod on AFE in photosensitive birds showed that the rates of response by turkey, partridge and quail were similar, with delays of 0.80, 0.82, and 0.88 d in AFE respectively for each 1 d delay in photostimulation, but that they contrasted with the more shallow responses ($\approx$ 0.41) of domestic fowl (Figure 3.10). The data for broiler breeders has been added since the original analysis by Lewis and Morris (1998*b*). It was suggested in that publication that the difference in rate of response between domestic pullets and other avian species indicated a difference between birds that did and those that did not
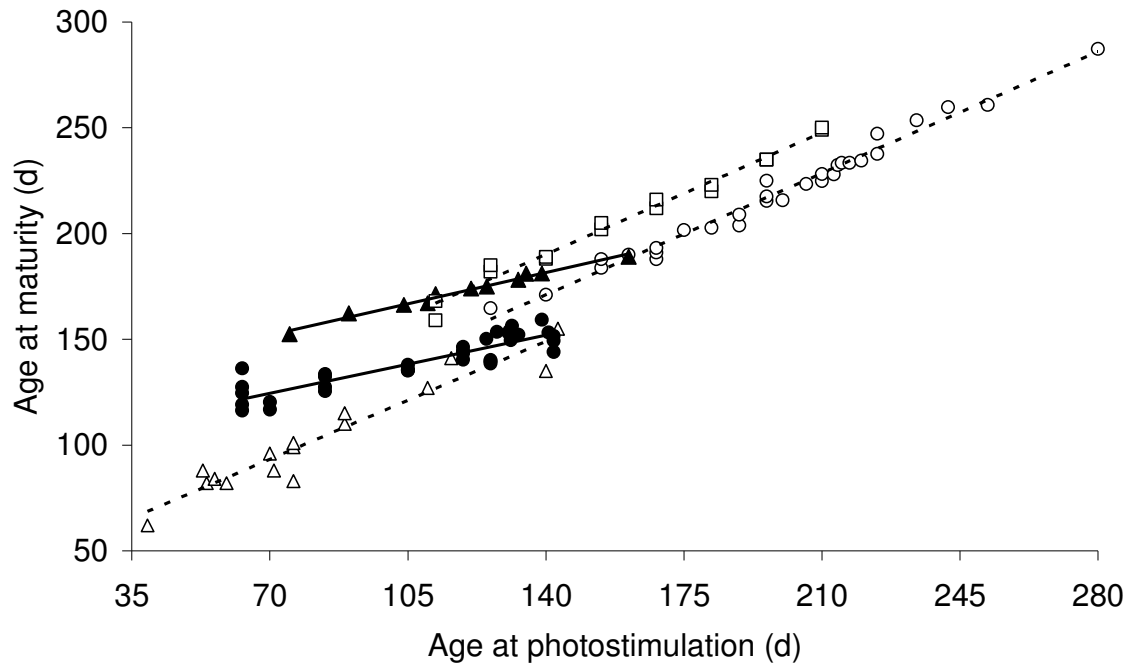
Figure 3.10 Regressions of age at sexual maturity on age at transfer to a stimulatory photoperiod for egg-type pullets (●), broiler breeders weighing 2.1 kg at 20 weeks (▲), turkeys (○), partridge (□), and quail (Δ), from Lewis and Morris (1998*b*).

exhibit photorefractoriness, however, the subsequent conclusion by Lewis *et al.*, (2003*a*) that broiler breeders exhibit photorefractoriness has discredited this hypothesis.

3.6 Lighting and performance in egg-type laying hens

Prepubertal lighting and photoinduced sexual maturity

Egg numbers, egg weight, and shell quality are all positively correlated with rearing photoperiod, but the correlations are more correctly with the age and/or body weight at sexual maturity induced by the lighting regimen rather than with photoperiod *per se* (Lewis *et al.*, 1994*c*, 2007*b*). The effect of ASM on various egg production traits was described by Shanawany (1983), however, the review was only for data produced between 1950 and 1975. Since that time, the genetic potential of egg-laying hybrids has changed markedly, with significant increases in egg numbers, advances in ASM, and improvements

in egg weight and feed conversion efficiency (Shalev, 1995); the increase in egg weight is rather remarkable because, genetically, the trait is negatively correlated with egg numbers.

Lewis *et al*. (1997*b*) calculated that a 10-d delay in AFE would result in a decrease of about 7 eggs per bird to 72 weeks of age, but with an increase of 1.3 g in mean egg weight. Shell quality and the incidence of mortality were not significantly affected by AFE, but feed intake was negatively, and feed conversion efficiency positively, correlated with AFE. Egg weight was strongly influenced by yolk weight, which was in turn closely associated with AFE. Lewis *et al*. (1998*e*) concluded that the yolk weight in single-yolked eggs increased by 0.92 g, and the combined weight of yolk in double-yolked eggs by 2.16 g, for each 10-d delay in AFE. Overall, it was concluded that the effects of ASM on laying performance in modern hybrids were little different from those identified by Shanawany (1983) for early strains of laying hens.

Photoperiod in the laying phase

The response to photoperiod in the laying phase appears to be independent of previous lighting history, with similar effects for birds maintained on a photoperiod from soon after hatch and those transferred to it at the end of the rearing period. The effects on egg numbers and egg weight are described in the section on constant photoperiods on pp. 30-33.

A meta-analysis of data from trials conducted by the author and others at the University of Bristol showed that both shell weight and shell thickness index (mg/cm²) were negatively correlated with photoperiod in lay (Figure 3.11). However, Lewis and Morris (2006, book) considered that the response was more correctly linked to the length of the dark period, because the consequential positive correlation provided a logical explanation for why hens given longer dark periods lay eggs with better shells; the two hormones involved in the mobilisation of calcium from the skeleton for shelling processes, calcitonin
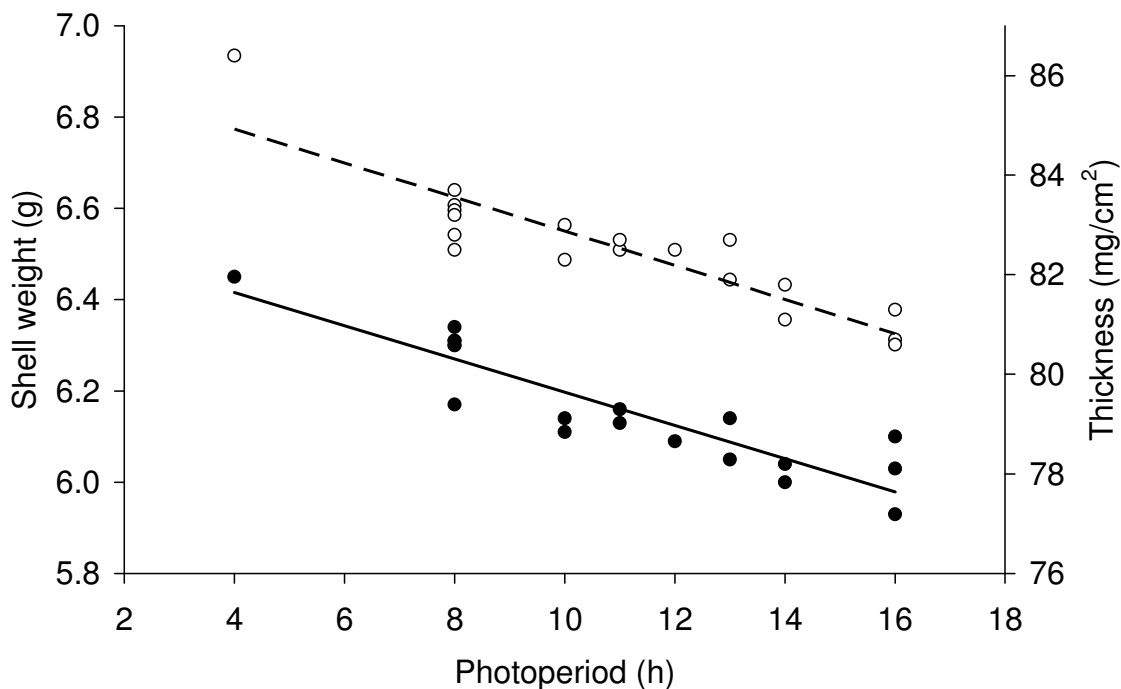
Figure 3.11 Regressions of shell weight and shell thickness index for egg-laying hybrids on photoperiod in the laying period (Lewis and Morris, 2006 - book)

and parathyroid hormone, each have peak releases at night, and so longer scotoperiods permit extended activity of these hormones.

Lewis *et al.* (1996*a*) reviewed data from trials conducted at the University of Bristol and from literature for the incidence of mortality in caged laying hens during a 52-week laying cycle and concluded that it was positively correlated with the amount of illumination, irrespective of whether the light was given in one or more than one period within a 24-h cycle. Lewis *et al.* (1994*a*) calculated that laying hens consume 1.2% more energy and increase their heat production per unit of metabolic weight by 1.4% for each extra 1-h illumination per 24 h, and so, despite there being only a trend for hens given longer periods of illumination to have higher body weights and larger carcass fat contents at end of lay, the positive correlation of mortality and light may still be a consequence, if only in part, of this photoperiodically stimulated energy intake.

Effect of a change in photoperiod during the laying cycle

Changes in photoperiod made during the laying year, especially reductions in daylength, invariably result in a change in rate of lay. It was not clear whether these changes were direct responses to the change in photoperiod itself, to photoperiodically induced changes in feed intake, or to a combination of each. Lewis *et al.* (1996*c*) studied the responses of white-egg and brown-egg hybrids to various changes in daylength and feeding opportunity at 32 weeks of age. The findings clearly showed that daily feed intake in *ad libitum*-fed hens was linearly related to the change in photoperiod (± 2.5 g per ± 1-h change in photoperiod), but that the neuroendocrine influence on rate of lay was dependent on the initial and final photoperiods rather than on any given change in photoperiod. The effects of the photoinduced changes in hormonal release were invariably larger than the effect of the changes in feed intake. The effects of changes in light and feeding opportunity on egg weight were complex, but the generalised conclusion was that egg mass output is linearly
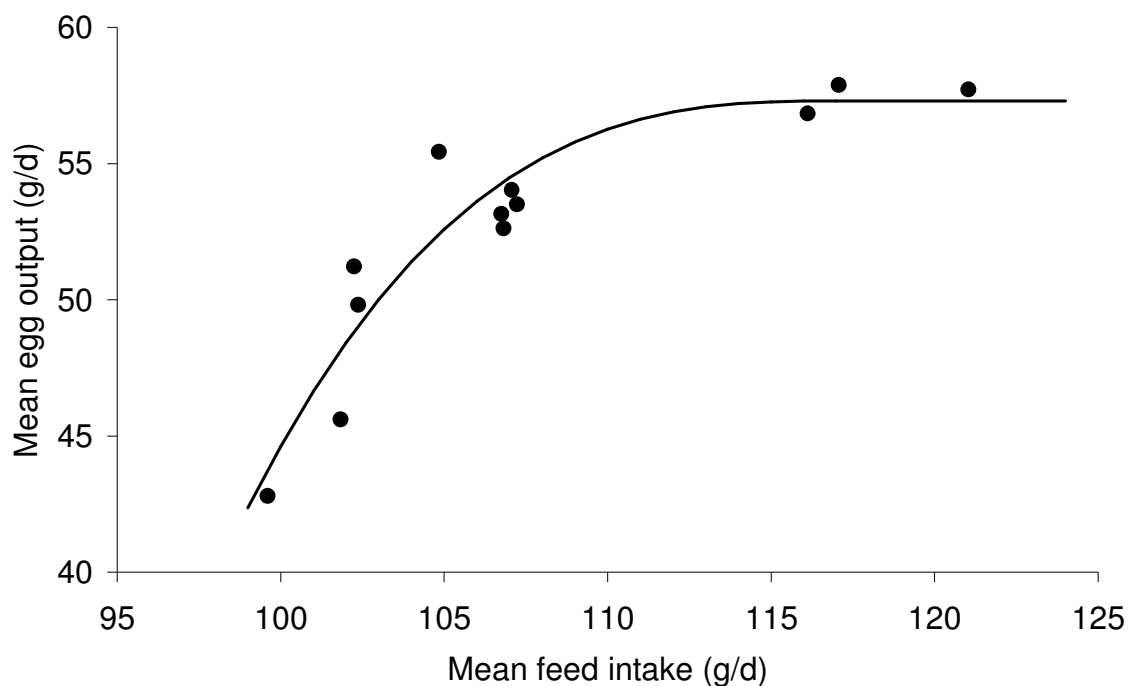
Figure 3.12 Regression of mean egg output of egg-laying hybrids on mean feed intake subsequent to a change in photoperiod at 32 weeks of age (Lewis *et al.* 1996*c*).

related to feeding opportunity and curvilinearly related to light, thus the relative importance of each influencing factor varies with the size and direction of the photoperiod change. The unquestionable involvement of feeding opportunity as well as light in the response of hens to changes in photoperiod, which was demonstrated by a typical nutritional response curve for egg output on feed intake (Figure 3.12), contradicted the earlier conclusion of Morris *et al*. (1964) that changes in feeding opportunity played no part in the determination of the response to changes in daylength.

3.7 Lighting and performance in broiler breeder hens

A regression of egg numbers to 60 weeks on ASM showed a highly significant negative correlation, with similar slopes for birds given either constant or changing photoperiods (Figure 3.13). A common regression for both types of lighting indicated that egg numbers are reduced by 3.8 eggs for each 10-d delay in ASM. It is surprising, therefore, that birds that have been transferred to 16 h and had their maturity advanced should consistently lay fewer eggs during the laying period than birds transferred to only 11 or 12 h (Lewis, 2006). The poorer production is most likely due to a combination of an earlier onset of adult photorefractoriness (Lewis *et al*., 2003*a*) and higher daily energy expenditure by the 16-h birds (MacLeod *et al*., 1988). Broiler breeders are given fixed daily allocations of feed, and so any reduction in maintenance afforded by 4 to 5 h less illumination (1 h less light $\approx$ 1% lower energy expenditure) potentially releases energy for productive purposes. In four studies at the University of KwaZulu-Natal, sexual maturity for birds transferred to 16 h was only 2.8 d earlier than for birds moved to 11 or 12 h, and this advance, on its own, would only be expected to result in one more egg to 60 weeks of age.

When broiler breeders are initially transferred to an 11- or 12-h final photoperiod at 20 weeks of age, before being given further increases to 16 h, egg production will be superior to that of birds transferred abruptly to 16 h (Lewis *et al*., 2007*f*). These findings
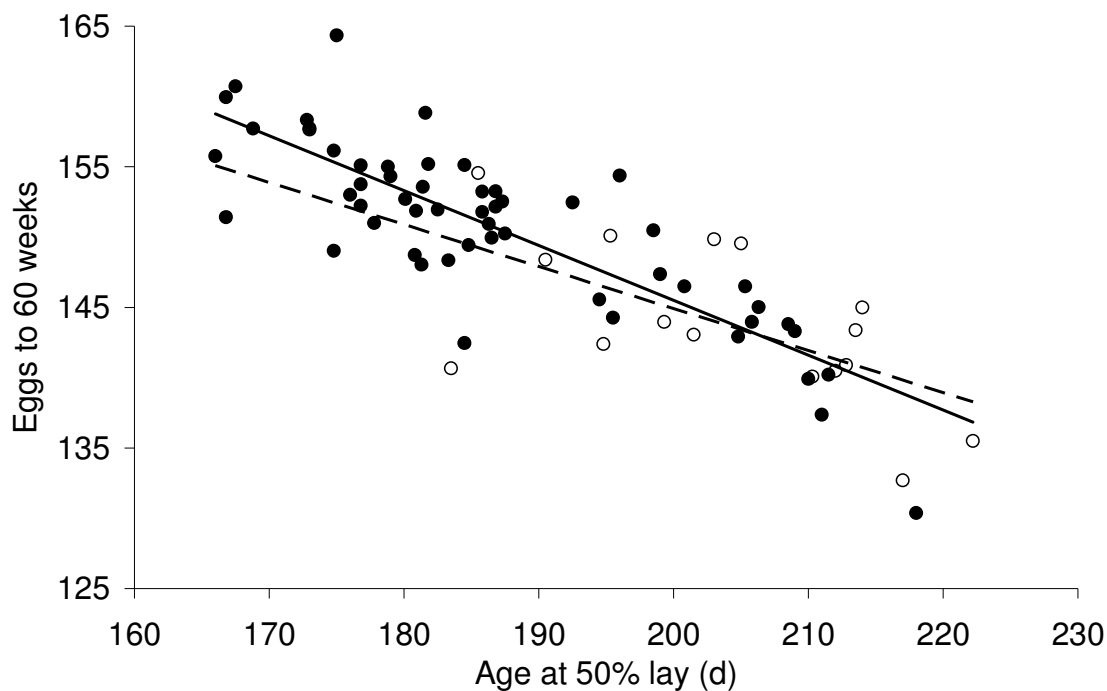
Figure 3.13 Regressions of egg numbers to 60 weeks on age at 50% lay for broiler breeders maintained on a constant photoperiod (○ and broken line) or transferred to a longer photoperiod at various ages (● and solid line) using 18 sets of data from studies conducted at the University of KwaZulu-Natal.
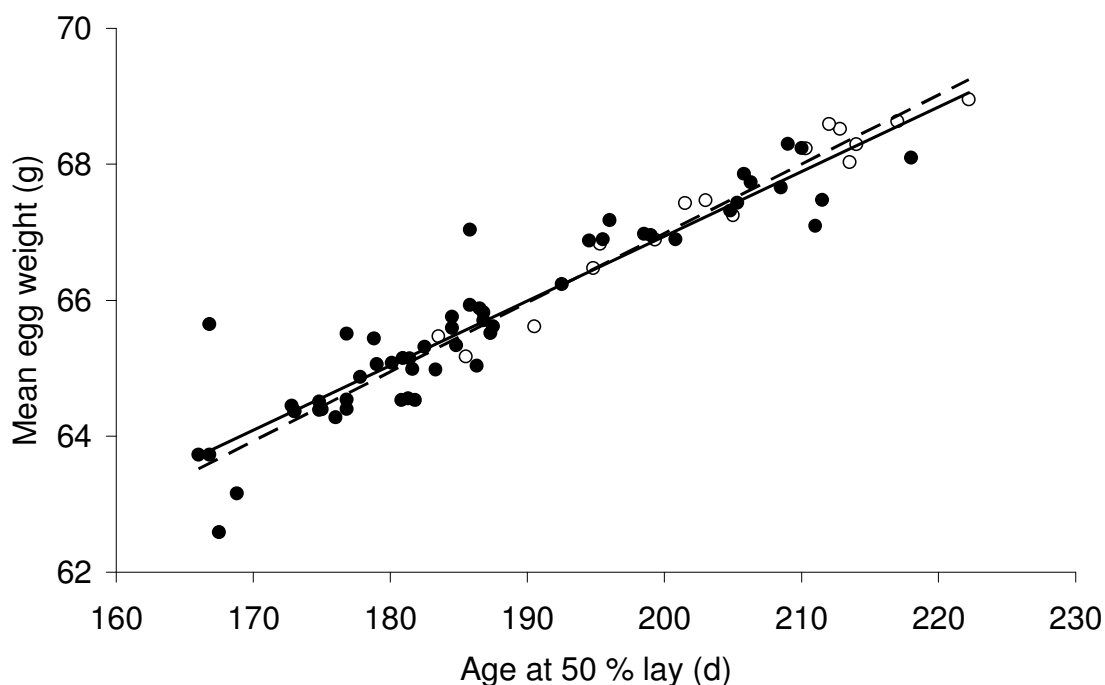
Figure 3.14 Regressions of mean egg weight to 60 weeks, adjusted to a 2.1-kg body weight at 20 weeks, on age at 50% lay for broiler breeders maintained on a constant photoperiod (○ and broken line) or transferred to a longer photoperiod at various ages (● and solid line), using 18 sets of data from studies conducted by the author at the University of KwaZulu-Natal.

supported the hypothesis of Dawson (2001) that the initial increase in daylength triggers the mechanisms for initiating both sexual maturation and the onset of adult photo-refractoriness, and that the processes continue to completion at a slower rate if the initial transfer is to a less stimulatory photoperiod.

An analysis of mean egg weight to 60 weeks of age indicated that both ASM and body weight at 20 weeks have highly significantly influences upon it, but that photoperiod in the laying phase *per se* has minimal effect. However, this is not to say that lighting is irrelevant, because it has an indirect effect through its influence on ASM. When photoperiod was dropped from the regression, mean egg weight was described by the equation:

$$MEW = 43.5 + 0.0969A + 1.974BW$$

where MEW = mean egg weight to 60 weeks (g), A = age at 50% lay (d), and BW = body weight at 20 weeks (kg). The effect of ASM on egg weight, adjusted to a 20-week body weight of 2.1 kg, is clearly demonstrated in Figure 3.14. The regressions also show, as for egg numbers, that it is immaterial whether the bird matures in response to a constant or to an increment in photoperiod.

4. ILLUMINANCE

4.1 Illuminance and sexual maturation in egg-type pullets

Morris (1967*b*) concluded, from two unreported trials conducted at the University of Reading, that light intensity during the growing period was unimportant because pullets could be successfully reared with either very high or very low light intensities.

Lewis *et al*. (1999*a*) reported the findings of a study that involved a larger number of treatments and a wider spread of illuminance (means varying from 0.05 to 10.8 lux) than the Reading studies (0.2 to 5.0). Brown-egg hybrids that had been illuminated from 1 d of age with an 8-h photoperiod at a mean intensity of 8.7 lux (5.5 to 10.8 lux) had the photoperiod augmented at 70 d (when *ad libitum*-fed egg-type pullets are most responsive to an increase in photoperiod) by two 3-h periods of dim light, one immediately before and the other after the main photoperiod. The rationale of this protocol was to detect the lowest illuminance at which the pullets interpreted the regimen at a 14-h day. A meta-analysis of the data for mean AFE, together with data from Reading University, indicated that whereas
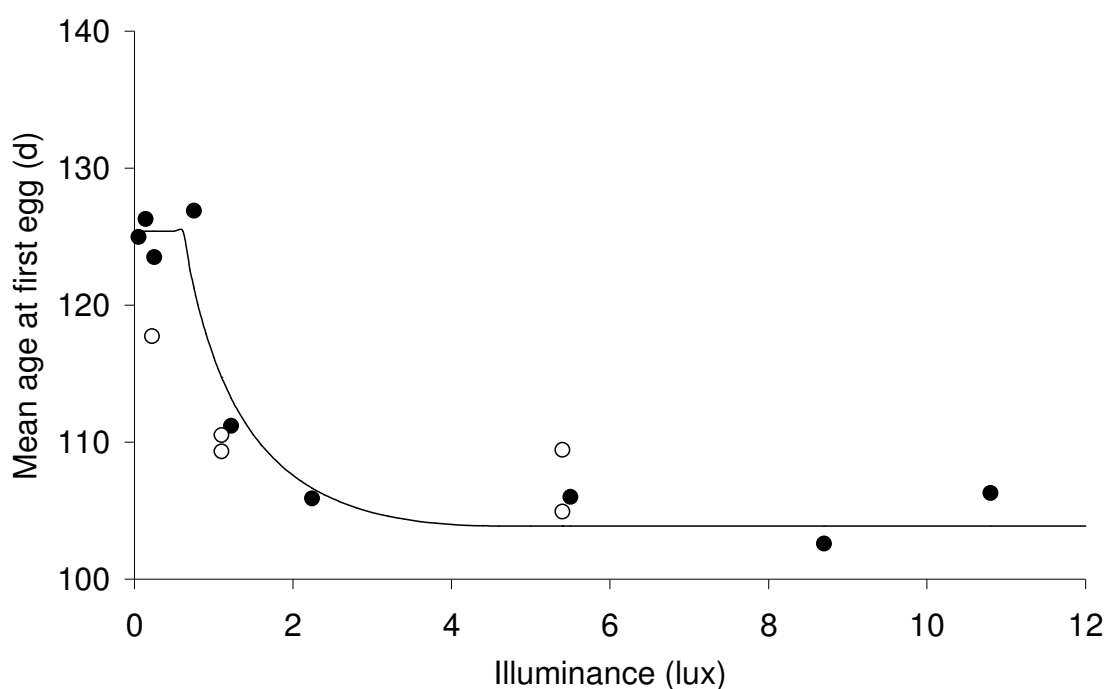
Figure 4.1 Regression of mean age at first egg on illuminance at the feed trough (●) Lewis *et al*., 1999*a*, and (○) unpublished data from University of Reading.

birds given supplementary light at ≥ 1.7 lux matured 30 d earlier than birds maintained on 8 h of normal intensity light, AFE in birds given supplementary light at ≤ 0.75 lux was still advanced by 10 d (Figure 4.1).

A change in photoperiod had been shown to exert a more potent influence on sexual maturation than the photoperiod itself (e.g., Whetham, 1933; Morris and Fox, 1958*b*; Lewis *et al*., 1996*d*), and light intensity *per se* had been demonstrated to modify the rate of sexual development (Figure 4.1), but there had been no reports for the effect of a change in illuminance on sexual maturation. Accordingly, Lewis *et al*. (2004*c*) studied the effects of an increase from 3 to 25 lux and a decrease from 25 to 3 lux at 63 or 112 d on age at sexual maturity in white-egg and brown-egg strains of egg-laying hybrid maintained on a constant 10-h photoperiod to 140 d. The 3-lux intensity was chosen because it exceeded the threshold for full photostimulation of sexual development (Lewis *et al*., 1999*a*), and the 25 lux because a similar contrast in illuminance (10:1) had been observed to stimulate the resumption of egg production in photorefractory partridges maintained on long-days (Siopes and Wilson, 1978). The ages at which the light intensities were changed were chosen because *ad libitum*-fed egg-laying pullets are most responsive to an increment in photoperiod at about 63 d and to a decrease in photoperiod at about 105 d (Lewis *et al*., 2002).

Unexpectedly, the increases in illuminance given at 63 and 112 d retarded sexual development whilst the reductions at 112 d advanced it; and white-egg hybrids had stronger responses than brown-egg birds. In contrast, increases in intensity at 63 d induced an increase in plasma LH within 4 d, but not at 112 d, whilst decreases in illuminance depressed circulating LH at both 63 and 112 d; responses similar to those expected for increases and decreases in photoperiod, and further demonstrations of the poor correlation of change in LH release with rate of sexual maturation. It was suggested that the

contrasting effects on gonadal development of changes in illuminance, compared with those expected in response to a change in photoperiod, were consequences of a phase-shift in the circadian rhythm of photoinducibility and/or a modification of the responsiveness of phototransduction pathways; the avian photosexual response has been shown, in partridge, to be more robust at low illuminance (when there is total reliance on the trans-cranial light pathway) than at brighter light intensities (when photoreception is both ocular and extra-retinal) (Siopes and Wilson, 1978).

4.2 Illuminance and sexual maturation in broiler breeders

There had been few prior studies of the effect of illuminance on the performance of broiler breeders (e.g., Proudfoot *et al*., 1984; Brake and Baughman, 1989; Renema *et al*., 2002). In two of the studies it had been concluded that at no stage of the broiler breeder's life did light intensity significantly affect reproductive performance, and, in the third, all birds had been reared at the same illuminance (10 lux) and transferred to 1, 5, 50 or 500 lux at 22 weeks. Whilst the more brightly illuminated groups matured significantly earlier than the lower-intensity groups, differences could have been due to the divergent changes in illuminance that occurred at 22 weeks and not to the prevailing light intensity. The wide spread of intensities also precluded the identification of an optimum illuminance.

Lewis *et al*. (2007*e*) reported that birds reared on 8-h days at 10 lux, prior to a transfer to open-sided housing, reached 50% egg production 2 d significantly later than birds reared at 40 or 100 lux, and, more importantly, had lower peak rates of lay which resulted in the production of 9 fewer eggs to 60 weeks. In a further, unreported study, birds reared at 44 lux reached 50% egg production 4 d significantly earlier than birds reared at 13 or 21 lux, suggesting that the optimum illuminance to achieve the earliest ASM might be about 40 lux.

4.3 Illuminance and laying performance in egg-type hens

The laying hen's response to illuminance was initially investigated at the University of Reading (Morris and Owen, 1966; Morris, 1967*b*). The universally quoted 0.4 lux minimum illuminance required to effect a rate of egg production greater than that achieved in complete darkness, and therefore the maximum permitted extraneous light in controlled environment houses, was concluded by Morris (1967*b*). Morris (1981) then suggested that 5 lux was the optimum illuminance for maximising the reproductive and economic performance of laying hens, though Hill *et al*. (1988), Morris *et al*. (1988) and Tucker and Charles (1993) later suggested that the figure for modern egg-laying hybrids was probably much lower. Although an analysis of the findings of the latter three studies showed that the fall away in egg production when illuminance dropped below the optimum was much less severe than observed in the earlier studies, the general conclusion of a 5-lux optimum intensity at the feed trough did not require amendment (Lewis and Morris, 1999).

The review by Lewis and Morris (1999) indicated that mean egg weight during the laying year decreases by 0.13 g for each 10 lux increase in feed-trough illuminance, and so has minimal commercial importance because intensively housed laying hens are unlikely to be kept at an illuminance much brighter than 10 lux. One possible explanation for the negative effect of illuminance on egg weight is the 0.2 g reduction in voluntary feed intake that occurs for each 10 lux increase in light intensity.

5. ULTRAVIOLET RADIATION

In common with other avian species, but in contrast to humans, domestic fowl posses a fourth retinal cone that has a peak sensitivity at about 415 nm (Govardovskii and Zueva, 1977) and oil droplets that permit the transmission of wavelengths within the UV-A range of electromagnetic radiation (Bowmaker *et al.*, 1997).

In the first of two studies of the mature laying hen's response to ultraviolet radiation, brown-egg hybrids were sequentially exposed to between 9 and 12 d of 8 h of white light only, 8 h of white light (7 lux) immediately followed by (a) 8 h of dim (0.4 lux) violet light, then (b) 8 h of dim violet light plus UV-A at 1.1×10^{-1} W/m², and finally a transfer to 16 h of white light only (Lewis *et al.*, 2000*a*). Only the transfer to 16 h of white light effected a phase-shift in oviposition time. In the second trial, laying hens were given continuous illumination for 14 d to allow them to hormonally 'free run' before being given 12 h of supplementary of UV-A radiation starting at either midday or midnight within the LL conditions. During the free-running period, eggs were laid randomly throughout the 24 h, which continued during the period of supplemental UV-A, irrespective of its temporal location. However, feeding activity, which was random across the 24 h for white-light-only controls, was depressed during the periods of supplemental UV-A provision in the experimental birds.

The lack of a phase shift in the ovulatory cycle when hens were given supplemental UV-A radiation immediately following a normal photoperiod and the lack of entrainment to a 12-h period of UV-A radiation in continuously illuminated hens demonstrated, in fowl what had previously been found in Mallard drakes, that UV-A radiation has a minimal effect on avian photosexual mechanisms (Benoit, 1964). It was presumed that this failure to affect photosexual responses was a consequence of the UV-A being either too short a wavelength or of too low an intensity to penetrate to the hypothalamus. However, the

depression of feeding activity during UV-A exposure was in agreement with the observation that circadian activity in the canary could be entrained by periods of UV-A (Pohl, 1992) and supports the hypothesis that UV-A acts primarily at the retinal level to stimulate avian behavioural responses only (Bennett and Cuthill, 1994).

6. INTERRUPTED LIGHTING REGIMENS

The interrupted lighting studies summarised below were conducted at the University of Bristol and their findings formed the basis of a thesis submitted for the award of a *Ph.D.* degree (Lewis, 1987).

6.1 Reproductive performance, body weight and composition

It was concluded that egg production and mean egg weight for brown-egg hybrids given an asymmetrical lighting regimen were similar to those of birds given an equivalent solidly illuminated regimen, but that feed intake was consistently lower than conventionally lighted hens. Though not statistically significant, the differences were of the magnitude reported in the literature and similar to those observed under commercial egg production conditions. Shell quality, unlike that of birds given symmetrical interrupted lighting, was no different from that of hens given a conventional light-dark cycle (Lewis and Perry, 1987*b*, 1990*a*). Body weights and fat contents at the end of the annual laying cycle, and the
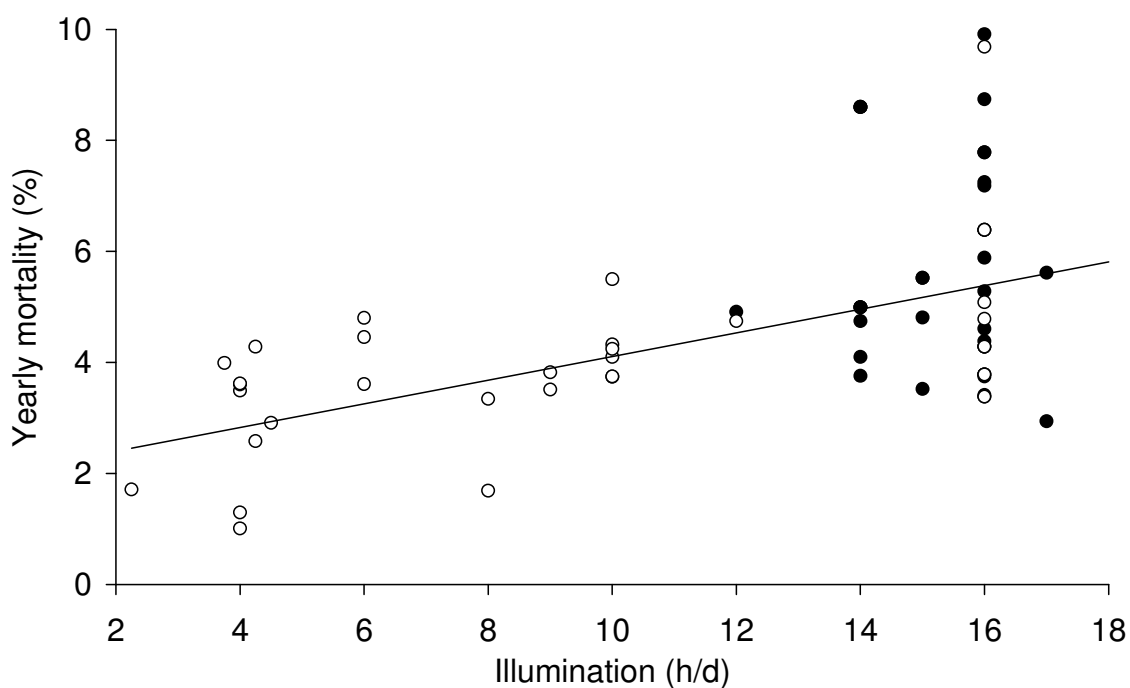
Figure 6.1 Effect of daily amount of illumination on the incidence of mortality in groups of laying hens given an intermittent (○) or conventional (●) lighting regimen (Lewis *et al.*, 1996*a*)

incidence of mortality caused by ruptured fatty livers were lower for intermittently illuminated hens than for conventionally illuminated controls (Lewis and Perry, 1989*a*).

An analysis of the incidence of mortality in the Bristol experiments and studies of various types of intermittent lighting regimen from the literature showed that, in general, intermittent lighting improved liveability compared with conventional lighting (Lewis *et al*., 1992). However, Lewis *et al*. (1996*a*) subsequently concluded that it was not intermittent lighting *per se* that improved liveability but the decreased amount of daily illumination; intermittent lighting regimens that did not involve a reduction in illumination were not associated with a reduced incidence of mortality (Figure 6.1).

6.2 Physiological influences

Patterns of diurnal noise output (Lewis *et al*., 1987) and feeding activity (Lewis and Perry, 1986), sleep and locomotor activity (March *et al.,* 1990), and daily rhythms of melatonin release (Lewis *et al*., 1989) clearly showed that laying hens interpret the longest scotoperiod in an asymmetrical interrupted regimen as night and the remainder of the 24-h cycle as day, whether the lights are on or off. Mean oviposition times, distributions of egg laying within the day, and the proportion of eggs laid in the modal 8 h were similar to birds given the equivalent solidly illuminated regimen (2L:4D:8L:14D ≡ 14L:10D), thus confirming that both groups used the same dark/light and light/dark interfaces as dawn and dusk respectively (Lewis and Perry, 1990*b*).

Although the reduction in daily feed intake for hens given asymmetrical interrupted lighting was not significantly different from normally lighted hens, the intermittent birds performed 25% less total daily feeding activity, consumed 20% of the daily intake during the scotoperiod(s) that formed part of the subjective day, and performed no feeding during the dark period that was interpreted as night (Lewis and Perry, 1986). Intermittent lighting

had no effect on crop weight or on the rate at which it was emptied (Lewis and Perry, 1990*b*).

Exposure of laying hens to an asymmetrical interrupted lighting regimen for a 52-week cycle did not result in the development of any ocular abnormalities (Lewis and Perry, 1990*b*).

6.3 Symmetrical intermittent lighting and red mite

A fortuitous observation following a study of the symmetrical intermittent lighting programme designed by Morris and Butler (1995) at the University of Reading (continuously repeating 15 min light and 45 min darkness) indicated that infestations of red mite (*Dermanyssus gallinae*) in houses given the experimental regimen were markedly lower than in those in which the hens had been given a 14L:10D regimen. It was suggested that this could have been a consequence of either the red mite's feeding opportunity being reduced by the very short scotoperiods (red mite only crawl on to hens at night to suck blood) to such an extent that they failed to ingest sufficient blood to sustain egg laying or that the mite's normal breeding cycle was disrupted by its inability to interpret a 24-h cycle; when all photoperiods and all scotoperiods are the same size in a lighting regimen, the hen cannot interpret a day and night, which results in many circadian oscillators, including the ovulatory cycle, 'free running' with 25.3-h rather than 24-h rhythmicity (Kadono *et al*., 1981).

In an experiment conducted at the University of Bristol to investigate the mode of action for the suppression of red mite breeding under intermittent lighting, laying hens were given a very short night within a conventional regimen (20L:4D), the original symmetrical intermittent regimen (24(15minL:45minD)), a more commonly used 4(3.5L:2.5D) symmetrical intermittent regimen, or a normal 14L:10D programme (Stafford *et al*., 2006). Data showed that whilst the short night of the 20L:4D regimen significantly

reduced red mite numbers, the principal factor to curtail red mite breeding was the intermittent nature of the lighting regimen; red mite were virtually eliminated from the two rooms in which the birds were intermittently illuminated (Figure 6.2).
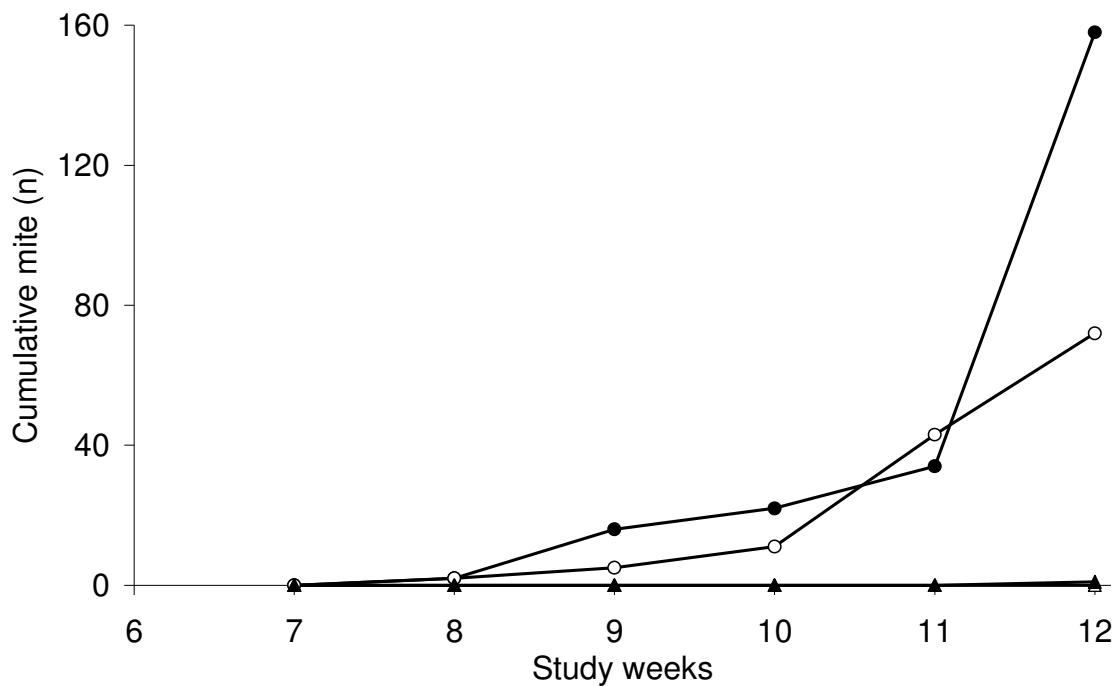

Figure 6.2 Cumulative numbers of trapped red mite in rooms of 25 hens exposed to 14L:10D (●), 20L:4D (○), 24(15minL:45minD) (▲) or 4(3.5L:2.5D) (Δ) for 12 weeks (data from Stafford *et al.*, 2006).

PUBLICATIONS

Those to which reference is made in the commentary are highlighted in bold type.

A. Refereed Journals (sole/senior author)

A1. LEWIS, P.D. (1987) Responses of Laying Hens to Interrupted Lighting Regimes. *PhD thesis*, University of Bristol.

A2. LEWIS, P.D. (2002) Lighting for commercial egg production. *British Poultry Science* 43: S6-S7.

A3. LEWIS, P.D. (2004) Responses of domestic fowl to excess iodine: a review. *British Journal of Nutrition* 91: 29-39.

A4. LEWIS, P.D. (2006) A review of lighting for broiler breeders. *British Poultry Science.* 47: 393-404.

A5. LEWIS, P.D. & GOUS, R.M. (2004) Effect of one or two pre-pubertal long-days on age at first egg in domestic pullets. *British Poultry Science* 45: 28-30.

A6. LEWIS, P.D. & GOUS, R.M. (2006a) Constant and changing photoperiods in the laying period for broiler breeders allowed normal or accelerated growth during the rearing period. *Poultry Science* 85: 321-325.

A7. LEWIS, P.D. & GOUS, R.M. (2006b) Effect of final photoperiod and twenty-week body weight on sexual maturity and egg production in broiler breeders. *Poultry Science* 85: 377-383.

A8. LEWIS, P.D. & GOUS, R.M. (2006c) Various photoperiods and *Biomittent*™ lighting during rearing for broiler breeders subsequently transferred to open-sided housing at 20 weeks. *British Poultry Science* 47: 24-29.

A9. LEWIS, P.D. & GOUS, R.M. (2006d) Abrupt or gradual increases in photoperiod for broiler breeders. *South African Journal of Animal Science* 36: 45-49.

A10. LEWIS, P.D. & GOUS, R.M. (2006e) Effect of temporary transfers to 14 h on age at first egg in domestic pullets reared on 8-h photoperiods. *British Poultry Science.* 47: 641-645.

A11. LEWIS, P.D. & GOUS, R.M. (2007a) Broilers perform better on short or step-up photoperiods. *South African Journal of Animal Science* 37: 90-96.

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A19. LEWIS, P.D. & MORRIS, T.R. (2004) Research note: amendments to the model for predicting age at sexual maturity for growing pullets of layer strains following changes in photoperiod. *Journal of Agricultural Science* 142: 613-614.

A20. LEWIS, P.D. & MORRIS, T.R. (2005) Change in the effect of constant photoperiods on the rate of sexual maturation in modern genotypes of domestic pullet. *British Poultry Science* 46: 584-586.

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A28. LEWIS, P.D. & PERRY, G.C. (1990b) Response of laying hens to asymmetrical interrupted lighting regimens: Physiological aspects. *British Poultry Science* 31: 45-52.

A29. LEWIS, P.D. & PERRY, G.C. (1990c) Glossary of avian photoperiodic terminology and methods of expressing lighting regimens. *British Poultry Science* 31: 677-684.

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A33. LEWIS, P.D. & PERRY, G.C. (1995a) An hypothesis for the phase setting of photosensitivity. *British Poultry Science* 36: 852-854.

A34. LEWIS, P.D. & PERRY, G.C. (1995b) Effect of age at sexual maturity on body weight gain. *British Poultry Science* 36: 854-856.

A35. LEWIS, P.D., PERRY, G.C. & TUDDENHAM, A. (1987) Noise output of hens subjected to interrupted lighting regimens. *British Poultry Science* 28: 535-540.

A36. LEWIS, P.D., PERRY, G.C. & COCKREM, J.F. (1989) Plasma concentrations of melatonin in layers under interrupted lighting. *British Poultry Science* 30: 968-969.

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