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Photoperiodic requirements for LH release in juvenile broiler and egg-laying strains of domestic chickens fed *ad libitum* or restricted diets

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Summary. Photoperiodic response curves for LH release were obtained for juvenile female domestic chickens at 8 weeks of age by measuring changes in plasma LH concentrations after increasing the daily photoperiod from 8 to 10·5, 12·75, 15·25, 17·75 or 20 h. The birds were bred either for meat production (broiler) or commercial egg-laying and were fed *ad libitum* or a restricted diet, similar to that used under commercial conditions. Ovarian and oviduct growth was stimulated by 2 weeks after transfer to 20 h light/day in the dwarf broiler strain, irrespective of the dietary treatment, but not in birds of the egg-laying strain. Baseline concentrations of plasma LH were higher in the egg-laying than in the dwarf broiler strain birds. A significant effect of dietary treatment was observed on the changes in concentration of plasma LH in the non-photostimulated dwarf broiler, but not in the egg-laying bird. There was no significant interaction between dietary treatment and photoinduced LH release in birds of either strain. The shortest photoperiod needed to stimulate LH release (critical daylength) was $< 10{\cdot}5$ h in the dwarf broilers and between 10·5 and 12·75 h in the egg-laying birds. The shortest photoperiod needed to stimulate the maximum release of LH (saturation daylength) was between 10·5 and 12·75 h in the dwarf broiler strain. The saturation daylength in birds of the egg-laying strain was longer, being between 12·75 and 15·25 h. It is concluded that there are differences in the photoperiodic response between chickens of different breeds and that they are not modified by restriction of food intake to 50–60% of that in control birds fed *ad libitum*.

Keywords: domestic chicken; LH; photoperiodism; restricted feeding

Introduction

The relationship between the rate of photoinduced gonadal growth and photoperiod in birds after transfer from short to long photoperiods shows considerable variation (Follett, 1984). At one extreme, in the white crowned sparrow (*Zonotrichia leucophrys gambelii*), testicular growth rate is proportional to photoperiods between approximately 12 and 20 h (Farner, 1964) while at the other extreme, in the Japanese quail (*Coturnix coturnix*), this relationship only holds for photoperiods betwen 11·5 and 14 h (Follett & Maung, 1978). The reason for this relationship has been established in the Japanese quail in which different rates of photoinduced testicular growth are directly related to increases of plasma FSH but not of plasma LH concentration (Follett & Maung, 1978). However, in the domestic chicken plasma LH concentrations are directly related to different patterns of photostimulation. Thus there was a direct relationship between concentrations of plasma LH and the duration of pulses of light given hourly to juvenile hens kept in 8 h light/16 h darkness, during the first 8 h of darkness (Wilson & Cunningham, 1980). It seems likely that concentrations of plasma LH could be used to establish in the domestic chicken whether, as in other

photoperiodic birds, there is a range of photoperiods within which there is a direct relationship with the photoinduced activation of reproductive function. Despite the many studies on the photoperiodic response of the domestic chicken (Morris, 1967, 1979; Sharp, 1984) this relationship has not been established. These studies did not define the minimum daylength required to stimulate gonadotrophin secretion (critical daylength) in chickens reared on short daylengths or the minimum daylength required to stimulate the maximum release of gonadotrophins (saturation daylength) (Sharp, 1984).

One of the factors which might alter the photoperiodic response is restriction in food intake. This technique is invariably applied to broiler-type breeding chickens for which it is necessary to control obesity (Pearson & Shannon, 1979). Although the practice delays sexual maturation (Buonomo *et al.*, 1982; Pearson & Herron, 1982; Whitehead *et al.*, 1987) and reduces numbers of yellow yolky follicles in the ovary (Hocking *et al.*, 1987), it also improves the rate of lay in the first and subsequent years. Food restriction may also be applied to egg-laying strain hens during the mid- to late-rearing stage to reduce food costs (Wells, 1978).

The objective of this study was to establish photoperiodic response curves for the release of LH in dwarf broiler and laying strains of commercial female chickens and to establish whether these are affected by dietary restriction, similar to that used under commercial conditions. To examine these questions two strains of hen were used, one a laying strain the other a dwarf broiler strain. It was anticipated that these two strains might react differently to the effects of feed restriction because of their different rates of growth.

Materials and Methods

Animals and experimental procedures. A dwarf broiler (PM3 dwarf broiler breeder, Ross Breeders Ltd, Newbridge, Lothian, UK) or a commercial egg-producing strain (ISA Brown, ISA Poultry Services Scotland, Thornhill, Dumfries and Galloway, UK) were obtained at 1-day-old and reared on the floor exposed to 8 h light per day with lights on at 08:00 h

The birds were fed a commercial starter diet throughout. The intake of half the birds of each strain was restricted to 50–60% of the intake of the remaining birds which were fed *ad libitum*.

The photoperiodic studies were carried out when the birds reached 8 weeks of age. At this age domestic chickens are fully responsive to photostimulation (Dunn *et al.*, 1990) and show no sign of rapid ovarian growth which may occur in older birds whilst maintained in short photoperiods (I. C. Dunn & P. J. Sharp, unpublished observations). At 4 days before the birds were 8 weeks old, they were randomly allocated on the basis of their weight into 6 treatment groups (N = 8) for each dietary treatment in both strains, and individually caged. At 8 weeks of age the photoperiod was increased to 10·5, 12·75, 15·25, 17·75 or 20 h of light per day, with a control group being maintained on 8 h light per day.

The daily photoperiod was increased by delaying the time at which the lights were switched off. Blood samples (1 ml) were taken from a wing vein between 12:00 and 14:00 h for the measurement of plasma LH on Days −2, −1, 0, +4, +5 and +6 with respect to the change in photoperiod.

The four control groups maintained on 8 h light per day and the four groups exposed to 20 h light per day were killed at 10 weeks of age, after 2 weeks of photostimulation, to weigh the ovaries and oviducts and thus give an indication of the effect of changes in plasma LH *in vivo*.

LH assay. Plasma LH was measured using the radioimmunoassay described by Sharp *et al.* (1987). The inter- and intra-assay coefficients of variation were 6 and 8% respectively. Sensitivity of the assay as measured by the ED_{80} was 0·10 ng/ml.

Statistical analysis. The experimental design produced three variables: strain, dietary restriction and photoperiod. A 3-way analysis of variance (ANOVA) was used to examine the effects of the variables and their interactions. Individual comparisons were made when indicated appropriate by the ANOVA using least significant difference and significance values were attributed using a *t* distribution.

The data for plasma LH were derived to give a single statistic (ΔLH) before ANOVA was performed. The means of the logarithms ($\log_{10}$) of the LH values from the 3 blood samples taken from each bird before and again after the change in photoperiod were calculated. The differences in the two mean logarithmically transformed LH values obtained for each bird were used to calculate photoinduced changes in plasma LH (ΔLH) levels in the different treatment groups. This elaborate sampling regimen and data transformation to normalize variation were necessary because preliminary studies showed that plasma LH concentrations are very variable, presumably due to a pulsatile pattern of release (Wilson & Sharp, 1975). Oviduct but not ovarian weights were also transformed to logarithms ($\log_{10}$) before further analysis.

All statistical comparisons on plasma LH were made on transformed data; however, the untransformed means are used in the text since it is felt they are more meaningful.

Results

Body weights

The body weights (mean ± s.e.m.) at 8 weeks of age for birds of the dwarf broiler and egg-laying strains fed *ad libitum* were 1271 ± 13 g (N = 48) and 680 ± 9 g (N = 48), respectively. The corresponding body weights of the birds fed the restricted diets were 742 ± 6 g (N = 48) and 481 ± 6 g (N = 48).

Ovarian and oviduct weights

Ovarian and oviduct weights were significantly increased, irrespective of dietary regimen, 2 weeks after transfer from 8 to 20 h light per day in birds in the dwarf broiler but not in the egg-laying strain (Table 1). In the dwarf broiler strain birds (Table 1) an analysis of variance indicated that there was a significant effect of food restriction on photoinduced ovarian and oviduct growth.

Table 1. The weights of ovaries and oviducts in female domestic chickens from an egg-laying or broiler strain 2 weeks after transfer at 8 weeks of age from 8 to 20 h light per day (8L→20L) or after being retained on 8 h light per day (8L→8L)

	Ovarian weight (g)		Oviduct weight (g)	
Photoperiodic treatment	Ad-libitum diet	Restricted food intake	Ad-libitum diet	Restricted food intake
Egg-laying strain				
8L→8L	286·0 ± 18·5	212·1 ± 32·9†	154·7 ± 11·5 (2·18)	89·6 ± 4·2 (1·95)†
8L→20L	351·6 ± 28·9	188·1 ± 10·7‡	226·6 ± 26·7 (2·33)	114·6 ± 7·9 (2·05)†
Broiler breeder strain				
8L→8L	371·0 ± 24·5*	219·4 ± 27·2‡	225·7 ± 23·1 (2·34)	154·2 ± 14·6 (2·18)
8L→20L	522·9 ± 18·6^{c,***}	308·8 ± 28·0^{a,**}†	1918·9 ± 584 (3·15)^{c,***}	777·4 ± 302 (2·75)^{c,***}‡

Values are means ± s.e. (N = 8). Values in parentheses are means of data transformed to logarithms ($\log_{10}$).

$^{a}P < 0{\cdot}05$; $^{c}P < 0{\cdot}001$ for comparisons between photoperiod within strain and diet; $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$ for comparisons between strain within diet and photoperiod; $\dagger P < 0{\cdot}05$; $\ddagger P < 0{\cdot}001$ for comparisons between diet within strain and photoperiod.

Standard error of the difference for ovary; 34·8. Standard error of the difference for oviduct; 0·11 (for log-transformed data).

Plasma LH

Mean (±s.e.m.) base-line concentrations of plasma LH before photostimulation were significantly higher in the dwarf broiler than in the egg-laying strain birds when fed *ad libitum*, 2·47 ± 0·11 and 1·66 ± 0·09 ng/ml respectively (N = 48, $P < 0{\cdot}001$), or when fed a restricted diet, 2·58 ± 0·15 and 1·94 ± 0·07 ng/ml respectively (N = 48, $P < 0{\cdot}01$). Non-photostimulated LH

values were significantly higher in dwarf broilers fed the restricted diet than in those fed *ad libitum*, 1·94 ± 0·07 and 1·66 ± 0·09 ng/ml respectively (N = 48, $P < 0·05$).

Table 2. Changes in the concentration of plasma LH after photostimulation with a range of daylengths at 8 weeks of age in female domestic chickens from an egg-laying or broiler strain reared from hatch in 8 h light per day

Type of chicken	Photoperiod‡ (h)	Change in plasma LH (ng/ml)	
		Ad-libitum diet	Restricted food intake
Egg-laying strain	8L→8·00L	−0·78 ± 0·29 (−0·14)	−1·10 ± 0·19 (−0·22)
	8L→10·50L	−0·86 ± 0·30 (−0·19)	−0·63 ± 0·30 (−0·13)
	8L→12·75L	0·76 ± 0·42 (0·12)[c]	1·00 ± 0·26 (0·16)[c]
	8L→15·25L	2·05 ± 0·54 (0·30)[c]	1·86 ± 0·36 (0·28)[c]
	8L→17·75L	1·61 ± 0·50 (0·19)[c]	1·92 ± 0·39 (0·25)[c]
	8L→20·00L	1·07 ± 0·57 (0·16)[c]	1·55 ± 0·49 (0·21)[c]
Broiler strain	8L→8·00L	−0·67 ± 0·15 (−0·16)	−0·08 ± 0·26 (−0·02)†**
	8L→10·50L	0·15 ± 0·10 (0·03)***	0·40 ± 0·14 (0·09)**
	8L→12·75L	1·40 ± 0·19 (0·28)[c,**]	2·10 ± 0·15 (0·34)[c,**]
	8L→15·25L	1·30 ± 0·16 (0·26)[c]	1·70 ± 0·20 (0·29)[c]
	8L→17·75L	1·42 ± 0·18 (0·27)[c]	1·75 ± 0·30 (0·26)[c]
	8L→20·00L	1·15 ± 0·17 (0·28)[c]	2·49 ± 0·39 (0·40)[c,**]

[c] $P < 0·001$ for comparisons with the control photoperiod within strain and diet.

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$ for comparisons between strain within diet.

† $P < 0·05$ for comparisons between diet within strain and photoperiod.

Values are means ± s.e. (N = 8). Values in parentheses are the means of values transformed to logarithms used in the statistical calculations. Standard error of the difference for transformed data; 0·067. The changes in plasma LH were calculated from the log-transformed mean of 3 samples taken at −2, −1 and 0 days before and at +4, +5 and +6 days after photostimulation.

Significance values were calculated using analysis of variance and Student's *t* test.

‡Birds were transferred from 8 h light/day (8L) to 10·5 (10·50L), 12·75 (12·75L), 15·25 (15·25L), 17·75 (17·75L) or 20 (20·00L) h light/day.

There was no effect of diet on non-photostimulated LH concentrations in birds of the egg-laying strain. Except for the restricted-diet dwarf broiler strain birds, concentrations of plasma LH decreased in birds kept in 8 h light/day during the course of the study (Table 2). When the changes in plasma LH between birds in the control photoperiod were compared, the value for broiler-strain birds fed a restricted diet differed from that for broilers fed *ad libitum* ($P < 0·05$) and from that for egg-layers on a restricted diet ($P < 0·01$) (Table 2).

Plasma LH concentrations increased significantly, irrespective of strain or dietary regimen, after increasing the daily photoperiod to 12·75, 15·25, 17·75 or 20 h (Table 2). There were significant effects of photoperiod ($P < 0·01$), dietary restriction ($P < 0·05$) and strain ($P < 0·01$) and an interaction between strain and photoperiod ($P < 0·01$) on photoinduced LH release.

There was no significant interaction between diet and photoinduced LH release in birds of either strain. The data for dietary treatment were therefore combined for birds within each strain to produce the LH photoperiodic response curves shown in Fig. 1. In the dwarf broiler-strain birds, the shortest photoperiod required to stimulate an increase in LH release (critical daylength) was 10·5 h light/day (Table 2, Fig. 1). In contrast, birds of the egg-laying strain required between 10·5 and 12·75 h light per day to stimulate a significant increase in the release of LH. The shortest photoperiod required to stimulate the maximum release of LH (saturation daylength) was between 10·5 and 12·75 h in the dwarf broiler-strain birds. However, the saturation daylength for the egg-laying birds was significantly longer, being between 12·75 and 15·25 h (Fig. 1).

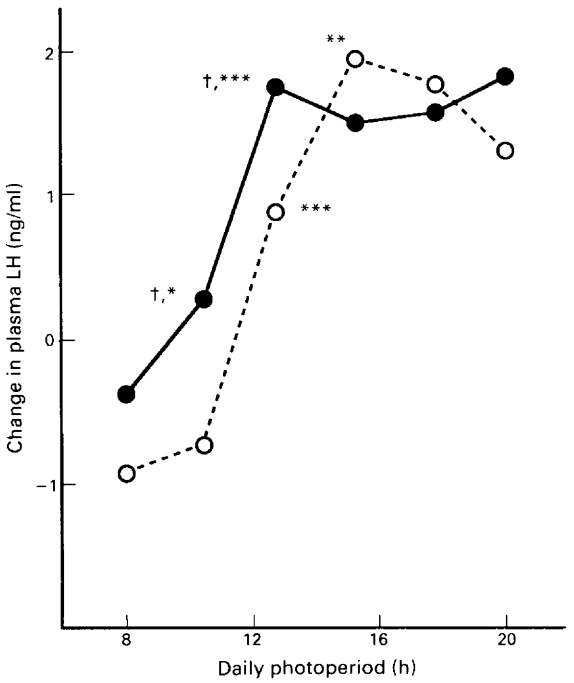

Fig. 1. Photoperiodic response curves for LH release in female domestic chickens from a broiler-type strain (●——●) or an egg-laying strain (○– – –○). The birds were reared in 8 h light/day and transferred at 8 weeks of age to the range of increased photoperiods shown. The change in the concentration of plasma LH (ΔLH) is plotted against the photoperiod to which the birds were exposed. *$P < 0·05$; **$P < 0·01$; ***$P < 0·001$ for comparisons within the same strain with the next shortest photoperiod. †$P < 0·01$ for comparisons with birds from the egg-laying strain exposed to the same photoperiod.

Discussion

The study shows that, in the domestic chicken, photoinduced changes in the concentration of plasma LH can be used to establish photoperiodic response curves (Fig. 1). The relationship between photoinduced LH release and photoperiod may only hold for a few days after photostimulation

because plasma LH concentrations are similar 11–14 days after transfer from 8 to 11, 12, 13, 14 or 20 h light per day (Sharp, 1988). In a similar study with Japanese quail, photoinduced changes in plasma LH were used to establish a photoperiodic response curve in castrated (Urbanski & Follett, 1982) but not in intact birds (Follett & Maung, 1978). It is likely that the design of the present study, which improved the accuracy of the measurement of mean plasma LH concentrations by taking into account the episodic pattern of LH release, made it possible to construct photoperiodic response curves for LH release in intact birds.

The photoperiodic response curves were extremely steep for birds in the dwarf broiler and egg-laying strains and in this respect are much more like the photoperiodic response curves for testicular growth in quail (Follett & Maung, 1978) than those in white-crowned sparrow (Farner, 1964). The steepness of the curves serves to emphasize the small difference between the shortest daylength required to stimulate gonadotrophin secretion (critical daylength) and the shortest daylength required to stimulate maximum gonadotrophin secretion (saturation daylength) (Sharp, 1984). However, the experimental design did not allow these to be defined to less than 1·5 h. Despite this poor resolution it was clear that the saturation daylength in the egg-laying strain (between 12·75 and 15·25 h) was longer than in birds of the dwarf broiler strain (between 10·25 and 12·75 h). This was an unexpected finding and presumably reflects the divergent ancestry of the two strains of bird. A difference in the photoperiodic response of birds of the same species has also been observed in finches breeding at different latitudes (Dol'nik, 1963).

The finding that restricted food intake did not significantly depress photoinduced LH release in birds of dwarf broiler or egg-laying strains is of interest because prolonged fasting depresses plasma LH concentrations in hens and cockerels from egg-laying strains of commercial chickens (Scanes *et al.*, 1976; Tanabe *et al.* 1981; Lal *et al.*, 1990). In contrast the dwarf broiler-strain birds had higher levels of baseline plasma LH when fed a restricted diet. This observation agrees with a previous study on the same strain (Dunn *et al.*, 1990). However, the observation that ovarian and oviduct weights were increased after 2 weeks exposure to 20 h light per day in the dwarf broilers given a restricted diet, but not in the restricted diet egg-layers (Table 1), indicates that food restriction may depress FSH release more in the egg-laying than in the dwarf broiler-strain bird.

Differences in baseline plasma LH concentrations between birds of dwarf broiler and egg-laying strains confirms earlier studies (Scanes *et al.*, 1980). In control non-photostimulated dwarf broilers fed *ad libitum* and egg-laying strain birds baseline plasma LH concentrations decreased during the course of the study. An explanation may be that LH values were depressed in response to stress associated with transfer of the birds from the floor pens to individual cages 4 days before photostimulation or with the handling required to take blood samples. This view finds support in the observation that movement of laying hens between cages depresses egg production (Glatz & Frensham, 1987) and, by inference, the secretion of gonadotrophins. There is no ready explanation for the greater decrease in non-photostimulated LH concentrations in the dwarf broiler strain when they were fed *ad libitum* than when they were fed a restricted diet. It is possible that restricted feeding is stressful for dwarf broilers and makes the birds less responsive to any further stress associated with handling.

The objective of many commercial lighting patterns is to bring hens progressively and synchronously into egg production by exposing them to small incremental changes in photoperiod each week (Morris, 1967, 1979). The present study suggests that the most effective increases should be between photoperiods of 10·25 and 12·75 h for birds of the dwarf broiler strain and between 10·25 and 15·25 h for birds of the egg-laying strain. Increases above this range at the beginning of a laying year, such as are commonly encountered in commercial lighting patterns, may have no direct effect on LH secretion and be largely superfluous. It appears that restriction of food intake, as practised commercially, does not affect the hen's photoperiodic response.

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