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Effect of constant photoperiods on the laying performance of broiler breeders allowed conventional or accelerated growth

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SUMMARY

An experiment was conducted at the University of KwaZulu–Natal to assess the effect of constant photoperiods on sexual maturity and egg-laying performance in broiler breeders given two levels of control-feeding during the rearing phase. Cobb broiler breeder females were grown to reach 2·1 kg body weight at 17 or 21 weeks, and maintained on 10, 11, 12, 13, 14 or 16-h photoperiods from 2 days to 68 weeks of age. There were no significant interactions between photoperiod and growth rate for any production parameter. The time required reaching 2·1 kg increased proportionally with photoperiod but, because of delayed sexual development, birds on longer photoperiods consumed more feed to, and were heavier at, sexual maturity than shorter daylengths. The longer-photoperiod birds also had inferior rates of lay in the first half of the cycle, but superior in the second, which, together with the photoperiodic effects on maturity, resulted in birds on 11, 13 or 14 h producing most eggs to 68 weeks, and those on 16 h fewest. It is possible that the pattern of egg production was due to some of the birds on $\geqslant$13-h photoperiods becoming photorefractory, having a mid-cycle pause, and then spontaneously resuming egg production in the latter half of the cycle. However, a hinge-analysis of current and other data to the more usual depletion age of 60 weeks showed that the combined effects of photoperiod on sexual maturity and egg production resulted in constant 10-h birds producing the highest number of eggs, with numbers decreasing by 3·6 eggs/h of photoperiod above the hinge and 7·8 eggs/h of photoperiod below it. Mean egg weight increased by 0·4 g/h of photoperiod, but the proportion of abnormally large and floor eggs and the incidence of mortality were unaffected by daylength. For each photoperiod, accelerated growth resulted in body weights being heavier than controls at sexual maturity, despite the mean age at maturity being 10 days earlier for the faster-growing birds. Body weights for the two growth groups were not significantly different at 68 weeks. Faster-growth birds consumed 1 kg less feed to 2·1 kg body weight, but 1·3 kg more feed to sexual maturity and 2·7 kg more to 68 weeks, and produced 6 more eggs than, but had similar patterns of egg production to, the conventionally managed controls. Mean egg weight, the proportion of floor eggs and the incidence of mortality were similar for both groups. Notwithstanding that the overall production of abnormally large eggs was low (1·1 eggs per bird); the faster-growing birds produced significantly more than the controls. Egg weight was positively influenced by age at sexual maturity, body weight at sexual maturity and photoperiod, but was unaffected by rate of growth to 2·1 kg per se.

These findings show that there are differences between broiler breeders and egg-type pullets in their response to constant photoperiods. It is likely that the factors responsible for these differences, particularly in terms of sexual development, are the exhibition of photorefractoriness by, and the retardational effects of controlled feeding on, broiler breeders.

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INTRODUCTION

Lighting programmes for domestic breeding fowl usually include one or more changes in daylength during the rearing period, and these exert a far greater

influence on sexual maturity than any of the photoperiods provided constantly (Morris 1967). Nevertheless, responses to constant photoperiods are important because they form an integral part of any model to predict the influence of lighting pattern upon sexual maturity and egg production. The effect of age at sexual maturity (ASM) on egg production is similar for the egg-and meat-type hens, decreasing by about 7 eggs for each 10-day delay in maturity (Lewis *et al.* 1997, 2003) but, because broiler breeders exhibit juvenile photorefractoriness, they mature differently from egg-type pullets when maintained on >10-h photoperiods from an early age (Lewis *et al.* 2003, 2004*a*). In egg-type layers, photoperiod also exerts an influence on egg production that is independent of maturity, and is typified by the rate of lay increasing linearly with photoperiod up to a plateau that starts variously at 10 h in white-egg, and 14 h in brown-egg hybrids (Lewis 1996). It is unlikely, however, to be a simple bent-stick response in broiler breeders because of the non-linear effect of >10-h photoperiods on ASM (Lewis *et al.* 2004*a*). Furthermore, the rate of onset of adult photorefractoriness has been reported to be inversely proportional to photoperiod in various avian species (e.g. quail – Robinson & Follett 1982; starlings – Dawson & Goldsmith 1983) and, if this occurs in broiler breeders, then this would add to the adverse effects of delayed maturity (Lewis *et al.* 2003).

Age at sexual maturity is advanced when broiler breeders are given a larger feed allocation than that normally recommended by a primary breeding company (Leeson & Summers 1983; Yuan *et al.* 1994; Nøddegaard *et al.* 2000; Gous & Cherry 2004) and it might be reasonably expected that advancing ASM would affect beneficially egg numbers. However, egg production has been disappointing when a relaxation of feed control has been combined with earlier-than-normal photostimulation, even when the birds have been photostimulated at similar body weights (Leeson & Summers 1983; Yuan *et al.* 1994). Undoubtedly, anomalies in ovarian function contribute towards the inferior reproductivity, with increases in the incidence of poly-follicular development, internal ovulation and follicular atresia when birds are given higher than normal feed allocations during the rearing period (Yu *et al.* 1992; Hocking 1993, 1996, 2004; Hocking *et al.* 2002; Gous & Cherry 2004).

McCluskey & Parker (1963) reported data for meat-type birds maintained on 1, 3, 9 or 13-h day-lengths, but there is a dearth of wide-ranging information for the response of modern meat-type breeders to constant photoperiods. The current paper reports the findings of an investigation that was conducted to study the effect of 10, 11, 12, 13, 14 and 16-h constant photoperiods on the performance of broilers breeders grown to achieve 2·1 kg body weight at 17 or 21 weeks (sexual maturity findings are reported elsewhere; Lewis *et al.* 2004*a*). Broiler breeder flocks are normally depleted at about 60 weeks of age, but these birds were kept to 68 weeks to allow the development, or otherwise, of adult photorefractoriness.

MATERIALS AND METHODS

A total of 3400 Cobb 500 broiler breeder females were equally, but randomly, distributed among 8 light-proof rooms in floor pens at 1 day of age (11·5 birds/m²); with each room subdivided into two pens by a wire netting partition. All rooms were given 2 days of continuous illumination before being permanently changed to a 10, 11 (2 rooms), 12 (2 rooms), 13, 14 or 16-h photoperiod, with all photoperiods beginning at 07·00. Mean illuminance produced by four 60 W incandescent lamps in each room was $26 \pm 2{\cdot}8$ lux at a height of 30 cm. At 10 weeks, 400 pullets from each of the rooms were transferred, without a change in photoperiod, to each of 8 adult light-proof rooms. There were 4 floor-pens in each room, two pens of birds on the enhanced feed allocation programme designed to achieve 2·1 kg at 17 weeks and, in the other two pens, birds fed to reach 2·1 kg at 21 weeks (8 rooms × 4 pens × 100 birds = 3200 birds). Stocking density was 5·0 birds/m² after the addition of males (1 per 10 females) at start of egg production. The 10, 13, 14 and 16-h photoperiod treatments were each represented in one room (2 pens × 100 normal-growth, and 2 pens × 100 accelerated-growth = 400 birds), and the 11 and 12-h photoperiod treatments were each represented in two rooms (2 rooms × 2 pens × 2 growths × 100 = 800 birds). Illumination was from a single 100 W incandescent lamp located in the centre of each pen, producing a mean light intensity of $25 \pm 4{\cdot}4$ lux at bird-head height.

All birds were fed a 210 g CP/kg, 12·4 MJ AME/kg crumbled diet *ad libitum* until transfer to a 175 g CP/kg, 11·9 MJ AME/kg pelleted diet scattered on the litter floor and controlled feeding at 3 weeks. At 6 weeks, the diet was changed to a 140 g CP/kg, 11·5 MJ AME/kg and finally to a 145 g CP/kg, 11·5 MJ AME/kg layer diet from 5% egg production onwards. Daily feed allocation was progressively increased to a peak of 170 g/bird/day at between 30 and 32 weeks, depending on rate of lay, before being reduced by 5 g/bird/day for each 5% fall in rate of lay in the final stages of the trial.

Egg numbers were recorded daily to pen, and eggs laid on a Monday, Wednesday and Friday bulk weighed. Age at sexual maturity for a pen was defined as the second day on which the total number of eggs for two consecutive days first reached or exceeded the bird numbers in the pen (equals 50 eggs/100 bird.day; %).

All data were subjected to a 2-way ANOVA using a model from *Genstat 6th Edition* (Lawes Agricultural Trust 2002), with photoperiod and growth as

variables. Mortality data were given an arcsine transformation before conducting the ANOVA. Significant differences between pairs of means were identified using a *t*-test and 2 degrees of freedom (df) for light comparisons and 18 df for the growth comparison. The reduced df for the photoperiod comparisons was used because only two of the treatments were room-replicated.

RESULTS

There were no significant interactions between the photoperiodic and growth treatments for any of the performance parameters measured and so, for clarity, results are described separately for each main effect. Sexual maturity data were reported in Lewis *et al.* (2004*a*) and are referenced, but not reproduced, in the current paper.

Photoperiod

Despite daily feed allocations being the same for all photoperiods within each growth-group, and body weight at 20 weeks not being significantly different among the various photoperiods (Table 1), there was a highly significant negative correlation of 20-week body weight with photoperiod described by the equation:

$$y = 2050 - 14p + 625G$$
$$(R^2 = 0{\cdot}994,\ P < 0{\cdot}001,\ \text{S.E.} = 4{\cdot}3) \qquad \text{(Eqn 1)}$$

where y = body weight at 20 weeks (g), p = photoperiod (h) and G = growth curve (normal = 0, accelerated = 1). Not surprisingly, body weight at sexual maturity (BWSM) was also correlated significantly with photoperiod (Table 1), increasing by about 60 g for each 1-h increase in photoperiod ($R^2 = 0{\cdot}744$, $P = 0{\cdot}004$, Slope S.E. = 16·0). However, the relationship would be correlated more correctly with the ASM that resulted from the photoperiodic influence, and for each of the growth-groups was described by the equations:

Normal growth

$$y = -754 + 20{\cdot}1SM$$
$$(R^2 = 0{\cdot}963, P < 0{\cdot}001, \text{Slope S.E.} = 1{\cdot}96) \quad \text{(Eqn 2}a\text{)}$$

Accelerated growth

$$y = 1353 + 11{\cdot}4SM$$
$$(R^2 = 0{\cdot}895, P = 0{\cdot}004, \text{Slope S.E.} = 1{\cdot}95) \quad \text{(Eqn 2}b\text{)}$$

where y = body weight at sexual maturity (g) and SM = age at sexual maturity (days). The +20 g/day slope of regression for the normal-growth birds (Eqn 2*a*) was significantly steeper than the +11 g/day for the faster-growth birds (Eqn 2*b*), but had 2100-g significantly lower intercept (Fig. 1). Body weights among the photoperiod groups were not significantly different at 68 weeks.

Table 1. *Body weight at 20 weeks, sexual maturity and 68 weeks (±S.E.M.) for Cobb 500 broiler breeder females maintained on a 10, 11, 13, 14 or 16-h photoperiod, and managed to reach 2·1 kg body weight at 17 or 21 weeks*

	Growth during rearing		
Photoperiod (h)	Accelerated	Standard	Photoperiod mean
Body wt at 20 weeks (kg)			
10	2·5	1·9	2·2 ± 0·19
11	2·5	1·9	2·2 ± 0·11
12	2·5	1·9	2·2 ± 0·12
13	2·5	1·8	2·2 ± 0·19
14	2·4	1·9	2·2 ± 0·16
16	2·5	1·8	2·1 ± 0·19
Growth mean	2·5 ± 0·02[a]	1·9 ± 0·01[b]	
Body wt at sexual maturity (kg)			
10	3·5	3·0	3·3 ± 0·13
11	3·4	3·2	3·3 ± 0·06
12	3·7	3·5	3·6 ± 0·06
13	3·7	3·5	3·6 ± 0·06
14	3·7	3·6	3·6 ± 0·03
16	3·6	3·5	3·6 ± 0·03
Growth mean	3·6 ± 0·04[a]	3·4 ± 0·05[b]	
Body wt at 68 weeks (kg)			
10	4·7	4·7	4·7 ± 0·07
11	4·8	4·9	4·8 ± 0·07
12	4·9	4·9	4·9 ± 0·06
13	4·7	4·9	4·8 ± 0·06
14	4·8	4·7	4·8 ± 0·04
16	4·7	4·8	4·8 ± 0·12
Growth mean	4·8 ± 0·03[a]	4·8 ± 0·05[a]	

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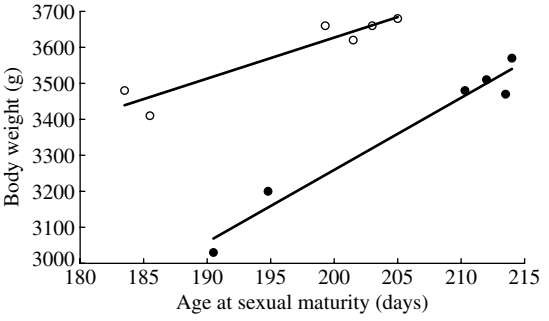

Fig. 1. Body weight (g) at sexual maturity (days) for Cobb 500 broiler breeder females fed to achieve 2·1 kg body weight at 17 (○) or 21 (●) weeks of age, and maintained on 10, 11, 12, 13, 14 or 16-h photoperiods.

Table 2. *Cumulative feed intake (kg) to 2·1 kg body weight, sexual maturity, and 68 week (± S.E.M.) for Cobb 500 broiler breeder females maintained on a 10, 11, 12, 13, 14 or 16-h photoperiod, and managed to reach 2·1 kg body weight at 17 or 21 weeks*

	Growth during rearing		
Photoperiod (h)	Accelerated	Standard	Photoperiod mean
2·1 kg body weight			
10	7·7	9·0	8·4 ± 0·40
11	8·1	8·9	8·5 ± 0·16
12	7·9	8·9	8·4 ± 0·22
13	7·7	9·0	8·4 ± 0·39
14	8·0	9·4	8·7 ± 0·48
16	8·7	9·6	9·1 ± 0·29
Growth mean	8·0 ± 0·11[a]	9·1 ± 0·08[b]	
Sexual maturity			
10	16·1	14·1	15·1 ± 0·60[a]
11	16·6	15·1	15·8 ± 0·32[ab]
12	18·5	17·4	17·9 ± 0·27[bc]
13	19·3	17·9	18·6 ± 0·41[c]
14	19·4	18·4	18·9 ± 0·45[c]
16	19·2	18·1	18·6 ± 0·36[c]
Growth mean	18·0 ± 0·34[a]	16·7 ± 0·42[b]	
68 weeks			
10	65·3	61·7	63·5 ± 1·09
11	65·4	62·5	64·0 ± 0·58
12	64·8	62·8	63·8 ± 0·44
13	64·5	62·2	63·3 ± 0·69
14	65·6	62·4	64·0 ± 0·93
16	65·1	62·9	64·0 ± 0·70
Growth mean	65·1 ± 0·14[a]	62·5 ± 0·16[b]	

Within a row or column, means with the same postscript are not significantly different at $P > 0{\cdot}05$.

Table 3. *Egg production data (± S.E.M.) to 68 weeks for Cobb 500 broiler breeder females maintained on a 10, 11, 12, 13, 14 or 16-h photoperiod, and managed to reach 2·1 kg body weight at 17 or 21 weeks. HD eggs = mean rate of lay (eggs per bird.day) × number of days*

	Growth during rearing		
Photoperiod (h)	Accelerated	Standard	Photoperiod mean
Total eggs to 68 weeks (HD eggs)			
10	166	172	169 ± 3·3[bc]
11	180	169	174 ± 3·2[a]
12	170	163	167 ± 2·2[c]
13	175	167	171 ± 2·7[b]
14	175	168	172 ± 3·6[ab]
16	169	164	166 ± 2·1[c]
Growth mean	173 ± 1·7[a]	167 ± 1·5[b]	
Rate of lay between 64 and 68 weeks of age (HD %)			
10	31	34	33 ± 1·0[c]
11	38	33	36 ± 1·5[bc]
12	41	35	38 ± 1·5[b]
13	44	42	43 ± 1·1[a]
14	44	46	45 ± 1·4[a]
16	40	45	43 ± 1·8[a]
Growth mean	40 ± 1·1[a]	38 ± 1·5[a]	
Abnormally large eggs (*n*)			
10	1·4	1·2	1·3 ± 0·07
11	1·4	1·1	1·2 ± 0·11
12	0·9	0·6	0·8 ± 0·06
13	1·0	0·6	0·8 ± 0·15
14	1·8	1·2	1·5 ± 0·18
16	1·6	1·3	1·4 ± 0·13
Growth mean	1·3 ± 0·09[a]	1·0 ± 0·08[b]	

Within a row or column, means with the same postscript are not significantly different at $P > 0{\cdot}05$.

There were significant effects of photoperiod on cumulative feed intake, with totals increasing by 0·12 kg to 2·1 kg body weight ($R^2 = 0{\cdot}914$, $P < 0{\cdot}001$, Slope S.E. = 0·031), and by 0·63 kg to 50% egg production ($R^2 = 0{\cdot}759$, $P = 0{\cdot}002$, Slope S.E. = 0·134), for each 1-h increase in daylength (Table 2). However, total feed intake to 68 weeks did not differ significantly for any of the photoperiod groups (Table 1).

There was a 22-day variation in mean ASM among the photoperiod groups, with 10-h birds reaching 50% lay at 187 days and 13-h birds at 209 days (Lewis *et al.* 2004*a*), and this had a significant influence on egg numbers, being described by the equation:

$$y = 227{\cdot}0 - 0{\cdot}40SM$$

($R^2 = 0{\cdot}634$, $P = 0{\cdot}002$, Slope S.E. = 0·096) (Eqn 3)

where y = total eggs to 60 weeks (typical depletion age for broiler breeders), and SM = age at 50% egg production (days). With the exception of the 14-h birds, those on 11-h photoperiods produced significantly more eggs to 68 weeks than any of the other photoperiod-groups, while 12 and 16-h birds produced least (Table 3). There were different patterns of egg production during the laying cycle among the various photoperiod-groups (Fig. 2), with birds on ⩽12-h photoperiods laying 8·5 more eggs than ⩾13-h birds to 45 weeks ($P < 0{\cdot}001$, Pooled S.E.D. = 3·97, Res, D.F. = 6), but 7·9 less eggs between 45 and 68 weeks ($P = 0{\cdot}022$, Pooled S.E.D. = 2·60, Res. D.F. = 6). The disparities were evident particularly between 64 and 68 weeks (Table 3) when, irrespective of

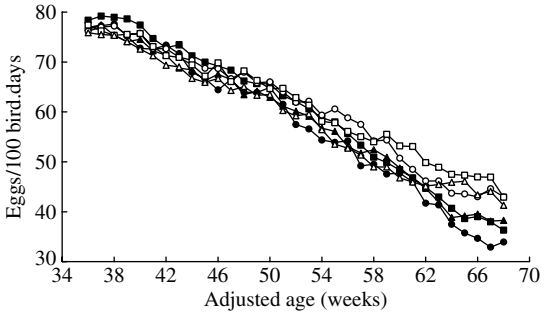

Fig. 2. Weekly rates of lay between 36 and 68 weeks (eggs/100 bird.days plotted against age adjusted to synchronize sexual maturities) for Cobb 500 broiler breeder females maintained on a 10 (●), 11 (■), 12 (▲), 13 (○), 14 (□) or 16-h (△) photoperiod (mean of standard and accelerated growth groups).

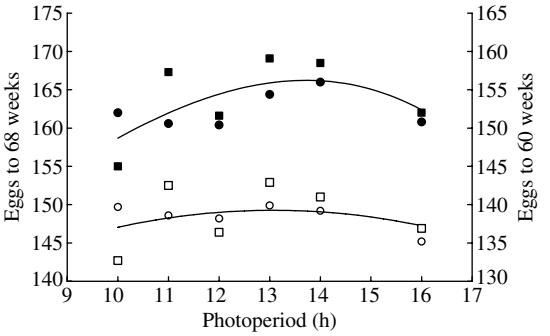

Fig. 3. Cumulative eggs for 201 days (open symbols) and 257 days (solid symbols) following sexual maturity for Cobb 500 broiler breeder females maintained on a 10, 11, 12, 13, 14 or 16-h photoperiod, and fed to achieve 2·1 kg body weight at 17 (squares) or 21 (circles) weeks of age.

growth group, rate of lay increased by 3·2% for each 1-h extension of daylength between 10 and 14 h ($R^2 = 0{\cdot}826$, $P < 0{\cdot}001$, S.E. = 0·52). To remove the effect of ASM (Eqn 3), so that the influence of photoperiod per se could be established, egg yields were compared for the same period post ASM. The slowest maturing pen of birds reached 50% lay at 219 days, and so 201 days (420–219) and 257 days (476–219) were selected for the 60 and 68-week age comparisons, respectively. A regression of egg numbers to 201 days post maturity on photoperiod was insignificant; however, eggs numbers to 257 days post maturity were strongly correlated with photoperiod (Fig. 3), and were described by the equation:

$$y = 124{\cdot}5 + 0{\cdot}666p^2 - 0{\cdot}0341p^3$$
$$(R^2 = 0{\cdot}456, P = 0{\cdot}064, \text{S.D.} = 3{\cdot}32) \qquad \text{(Eqn 4)}$$

where y = eggs laid until 257 days after sexual maturity, and p = photoperiod (h). Generally, the incidence of visually, abnormally large eggs (including double-yolked) was low (1·1 eggs per bird), and was not significantly affected by photoperiod (Table 3). Although birds on ⩽12 h daylengths commenced daily egg-laying before dawn (Lewis *et al*. 2004*b*), the proportion of eggs laid on the floor was not significantly affected by photoperiod. Mean egg weight to 68 weeks increased progressively with photoperiod, with 14 and 16-h birds producing eggs that were significantly heavier than 10-h birds (Table 4). A regression of mean egg weights for the two growth groups on photoperiod was described by the equation:

$$y = 65{\cdot}8 + 0{\cdot}41p$$
$$(R^2 = 0{\cdot}707, P < 0{\cdot}001, \text{S.D.} = 0{\cdot}08) \qquad \text{(Eqn 5)}$$

where y = mean egg weight to 68 weeks (g), and p = photoperiod (h). Although 13 and 14-h treatments produced significantly more egg output than 10-h birds, the differing effects of photoperiod on egg weight and egg numbers meant that there was no clear pattern for the effect on egg mass (Table 4).

Birds on 13 and 14-h days converted feed (including that consumed during the rearing period) into egg weight (g/g) significantly more efficiently than 10, 12 or 16-h photoperiods, while 11 and 13-h birds used significantly less feed to produce an egg than 10, 12 or 16-h birds (Table 4). Mortality was not significantly affected by photoperiod.

Growth

The accelerated group reached 2·1 kg at 116 days (slightly ahead of target), and the conventionally grown group at 150 days (slightly behind target). Body weights for the accelerated growth groups were significantly heavier than the standard body weight groups at both 20 weeks and sexual maturity, but were not significantly different at 68 weeks (Table 1). The faster-growing birds consumed 1·1 kg less feed to 2·1 kg body weight, but 1·3 kg more to 50% egg production, and 2·7 kg more through to 68 weeks than the conventional grown birds (Table 2).

The accelerated-growth birds, which matured 10 days earlier (195 *v*. 205 days), produced 6 more eggs to 68 weeks than the conventionally grown groups (Table 3), but peak and subsequent rates of lay for the two groups were similar (Fig. 4). Rather surprisingly, despite the accelerated-growth birds having a heavier BWSM than the conventionally grown birds, egg weights for the two groups were not significantly different (Table 4). However, the combination of a similar egg weight and superior egg numbers resulted in the accelerated-growth birds producing a significant 450-g larger total egg mass output to 68 weeks than the conventionally grown birds. The faster-growing

Table 4. *Egg weight, egg mass, and feed conversion data (± S.E.M.) for Cobb 500 broiler breeders maintained on a 10, 11, 12, 13, 14 or 16-h photoperiod and managed to reach 2·1 kg body weight at 17 or 21 weeks*

	Growth during rearing		
Photoperiod (h)	Accelerated	Standard	Mean
Mean egg weight (g)			
10	70	69	$70 \pm 0{\cdot}4^{b}$
11	70	70	$70 \pm 0{\cdot}2^{ab}$
12	72	72	$72 \pm 0{\cdot}2^{ab}$
13	72	71	$72 \pm 0{\cdot}2^{ab}$
14	72	72	$72 \pm 0{\cdot}1^{a}$
16	72	72	$72 \pm 0{\cdot}2^{a}$
Growth mean	$71 \pm 0{\cdot}3^{a}$	$71 \pm 0{\cdot}3^{a}$	
Total egg mass (kg)			
10	11·6	11·9	$11{\cdot}8 \pm 0{\cdot}19^{b}$
11	12·6	11·8	$12{\cdot}2 \pm 0{\cdot}22^{ab}$
12	12·1	11·7	$11{\cdot}9 \pm 0{\cdot}16^{ab}$
13	12·5	11·9	$12{\cdot}2 \pm 0{\cdot}21^{a}$
14	12·6	12·1	$12{\cdot}3 \pm 0{\cdot}24^{a}$
16	12·1	11·8	$12{\cdot}0 \pm 0{\cdot}15^{ab}$
Growth mean	$12{\cdot}3 \pm 0{\cdot}11^{a}$	$11{\cdot}83 \pm 0{\cdot}10^{b}$	
Feed per egg mass (g/g)			
10	5·6	5·2	$5{\cdot}4 \pm 0{\cdot}14^{a}$
11	5·2	5·3	$5{\cdot}3 \pm 0{\cdot}09^{bc}$
12	5·4	5·4	$5{\cdot}4 \pm 0{\cdot}07^{ab}$
13	5·1	5·2	$5{\cdot}2 \pm 0{\cdot}04^{c}$
14	5·2	5·2	$5{\cdot}2 \pm 0{\cdot}08^{c}$
16	5·4	5·34	$5{\cdot}4 \pm 0{\cdot}05^{ab}$
Growth mean	$5{\cdot}3 \pm 0{\cdot}05^{a}$	$5{\cdot}3 \pm 0{\cdot}05^{a}$	
Feed conversion per egg (g)			
10	394	359	376 ± 12^{b}
11	363	371	367 ± 6^{d}
12	382	385	384 ± 5^{a}
13	368	373	371 ± 2^{cd}
14	375	371	373 ± 7^{bc}
16	386	384	385 ± 3^{a}
Growth mean	377 ± 4^{a}	375 ± 4^{a}	

Within a row or column, means with the same postscript are not significantly different at $P > 0{\cdot}05$.

birds had a 0·3-egg significantly higher incidence of abnormally large eggs (Table 3). Incidences of mortality, and conversion of feed (including that consumed during the rearing period) into egg or egg weight were unaffected by growth during the rearing period (Table 4), however, regressions of each measurement of feed conversion on egg numbers showed that for a given number of eggs, birds allowed accelerated growth were less efficient than conventionally reared birds (Fig. 5).

DISCUSSION

In contrast to the results of other trials conducted at the University of KwaZulu–Natal, when broiler breeder pullets were grown to different 20-week body weights and given different increments in photoperiod at various ages, in the current trial, where the photoperiods were constant, there were no interactions between photoperiod and growth. It is likely that the interactions observed in the other trials were produced by different rates of growth facilitating different rates of juvenile photorefractoriness dissipation within each photoperiodic regimen, resulting in birds being at different stages of photo-responsiveness when they were transferred to photoperiods which themselves varied in stimulatoriness.

Photoperiod

The negative correlation of 20-week body weight with photoperiod (Eqn 1), irrespective of prepubertal growth and despite birds within the same growth group being given the same amount of feed, indicates

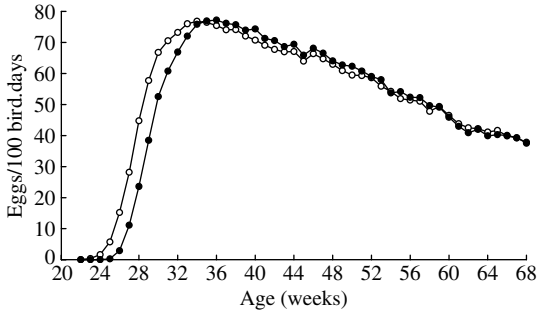

Fig. 4. Weekly rates of lay (eggs/100 bird.days) for Cobb 500 broiler breeder females fed to achieve 2·1 kg body weight at 17 (○) or 21 (●) weeks of age (means for birds maintained on 10, 11, 12, 13, 14 or 16-h photoperiods).

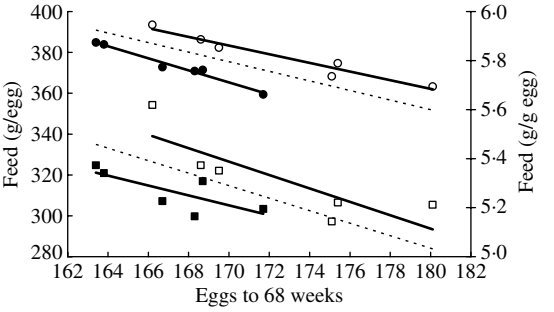

Fig. 5. Regression of feed (g) required to produce an egg (circles) and a gram of egg (square symbols) on eggs laid to 68 weeks for Cobb 500 broiler breeder females fed to achieve 2·1 kg body weight at 17 (open symbols) or 21 (closed symbols) weeks of age, and maintained on 10, 11, 12, 13, 14 or 16-h photoperiods. The dotted lines represent the mean changes in feed requirement for the two growth groups.

that daylength exerts its own influence on growth. A regression of feed required to reach 2·1 kg on photoperiod indicated that birds ate 1·2 % more feed, irrespective of growth pattern, for each 1-h extension of daylength ($P<0·001$). As birds expend about 1 % more energy during an hour of light than darkness (MacLeod *et al.* 1988), it is likely that the improved efficiency of birds on the shorter photoperiods was a consequence of a reduced demand for energy.

The 0·4-egg rate of decrease in egg numbers for each 1-day delay in ASM (Eqn 3) was lower than the 0·7 rate reported for broiler breeders to 56 or 58 weeks (Lewis *et al.* 2003), or for egg-type hybrids to 72 weeks (Lewis *et al.* 1997). However, in these earlier trials, the birds had been reared on 8 h daylengths prior to being transferred to various photoperiods, resulting in a more rapid and uniform dissipation of juvenile photorefractoriness for the broiler breeders, and wider range of sexual maturities than in the current trial, and this may have contributed towards the discrepancy. Nevertheless, the reported data still demonstrate the negative influence of a delay in ASM on egg numbers. The data in Fig. 3 show that the degree to which photoperiod influences egg numbers depends on the age at which performances are compared, especially if they are kept beyond the normal 60-week depletion age. Even though the apogee of photoperiodic influence occurred between 13 and 14 h for both comparisons, and was in agreement with the 14 h reported as optimal for brown-egg hybrids (Lewis 1996), the reduction in egg numbers when broiler breeders were given photoperiods longer than 14 h is in contrast to the plateau reported for egg-type hybrids. Notwithstanding that these responses were for birds held on constant photoperiods from a young age (not photostimulated at around 20 weeks), this questions the need to give daylengths that are longer than 14 h to birds kept in light-proof housing.

A hinge analysis of total egg production to the more typical depletion age of 60 weeks, together with

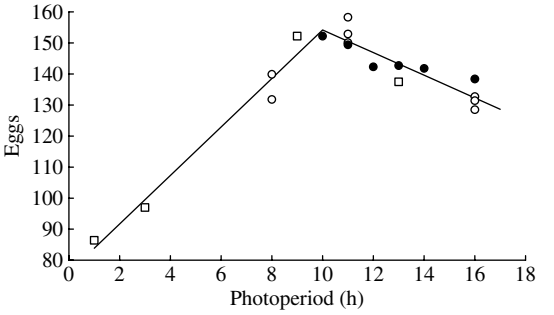

Fig. 6. Cumulative eggs produced to ⩽60 weeks of age for meat-type pullets maintained on constant photoperiods (● = current trial to 60 weeks, ○ = Lewis *et al.* 2003, □ = McCluskey & Parker 1963).

data from Lewis *et al.* (2003) and McCluskey & Parker (1963), was performed to identify the overall effect of constant photoperiod on egg production (including any effect of photoperiod on maturity), with differences from the current trial removed by fitting constants by least squares. Fuller details of this analytical procedure are given in Lewis *et al.* (1998), but this procedure enables the simultaneous use of more than one data set to identify the point at which there is a change in response to input, which in the current case was photoperiod. After iteration at intervals of 0·25 h, the optimal hinge point was found to be 10 h, with egg numbers decreasing by 7·8 eggs/h below the hinge, and by 3·6 eggs/h above it (Fig. 6). This shows that the advance in ASM achieved by maintaining birds on 10-h photoperiods (Lewis *et al.* 2004*a*), at least from a young age, outweighs the superior egg production in the latter stages of the laying period of birds given 13 and 14-h photoperiods (Eqn 4). Although egg production on 16-h daylengths

(and possibly longer), at least to 60 weeks of age, was adversely affected by both a delay in maturity and a photoperiodically induced reduction in egg numbers, it must be remembered that the current trial studied responses to constant photoperiods. The optimal photoperiod for the laying period might be different for birds that have been reared on short daylengths (which will have rapidly dissipated juvenile photorefractoriness) and transferred at about 20 weeks to a stimulatory daylength, or to a mildly stimulatory photoperiod with further increments given later in the laying cycle (Sharp 1988, 1993).

The inferior initial rate of lay by birds on longer photoperiods, but superior egg production later in the laying cycle, was also observed in Delaware meat-type birds maintained on 9 or 13-h daylengths (McCluskey & Parker 1963). In addition, data from Sharp *et al.* (1992) for dwarf broiler breeders exposed to 14-h photoperiods indicated that the proportion of birds out of lay stabilized at approximately 0·25 and egg production levelled out at about 0·30 from about 54 weeks of age through to the end of the trial at 64 weeks. Whilst these observations might suggest that prolonged exposure to long days does not induce adult photorefractoriness in meat-type domestic fowl, it is more probable that broiler breeders do become photorefractory but that, as in domestic turkeys, it is a relative form of photorefractoriness, and not absolute as manifest in seasonal-breeding wild birds, like starlings. Siopes (2001) reported that 0·84 of turkeys that had been transferred from 8 to 16 h at 30 weeks, and had subsequently stopped laying, spontaneously resumed egg production despite being held on the long days, and concluded that their photorefractoriness was not permanent. The current broiler breeders were not individually recorded, so it is not possible to conclude categorically that a similar situation exists in broiler breeders, but it would be a reasonable explanation for the resurgence in rate of lay by the longer-photoperiod hens in the current trial and by the 13-h birds studied by McCluskey & Parker (1963). To confirm the presence of photorefractoriness, it would be necessary to demonstrate no change in gonadotrophin concentration in out-of-lay birds following a photoperiodic challenge in the middle of the laying period, but a photoinduced increase in gonadotrophin release after transfer to a longer photoperiod in the final stages when birds had resumed lay. Unfortunately, this was not possible in the current trial. Although it is not possible to be confident of the reasons for the age-related differences in rate of lay between the shorter and longer daylength groups, it is possible that the inferior production of hens on the longer photoperiods during the first half of the production cycle (Fig. 2) was due, in part, to a proportion of the birds having an extremely late ASM. Lewis *et al.* (2003) reported that some birds on constant 16 h did not mature until nearly 40 weeks, while the poorer persistency of birds on shorter daylengths might be attributed, in part, to the photoperiods' lower photoperiodic drive (Sharp 1993). However, the steady decline in rate of lay through to 68 weeks for these shorter-daylength birds suggests that their poor persistency was more likely to have been caused by the naturally occurring, age related, increase in the number of yellow-yolky follicles that fail to ovulate and yolks that are laid internally, and to an increased production of shell-less eggs (Williams & Sharp 1978). Alternatively, though a little pedantic, it may have been that the longer-daylength birds simply laid at a better rate in the latter part of the laying cycle because a proportion of birds had spontaneously resumed laying after having had a pause, as discussed above, and others may have only recently become sexually mature following protracted dissipation of juvenile photorefractoriness.

The 0·4-g increase in mean egg weight for each 1-h longer photoperiod (Eqn 5), irrespective of the age at which birds reached 2·1 kg body weight, was higher than the 0·1 to 0·2 g/h rate reported for egg-type hybrids (Lewis 1996). However, the increase in egg weight is likely to have been a response to the later age and heavier body weight at 50 % lay, as well as being an effect of photoperiod per se. A multiple regression of egg weight on BWSM, ASM and photoperiod was described by the equation:

$$y = 52{\cdot}0 + 2{\cdot}259BW + 0{\cdot}042A + 0{\cdot}109p$$
$$(R^2 = 0{\cdot}969, P < 0{\cdot}001, \text{S.D.} = 0{\cdot}210)$$
$$(\text{S.E. values: } BW = 0{\cdot}405, A = 0{\cdot}008, p = 0{\cdot}049) \qquad \text{(Eqn 6)}$$

where y = mean egg weight to 68 weeks adjusted for growth (g), BW = body weight at 50 % lay (kg), A = age at 50 % lay (days), and p = photoperiod (h). The 0·109 g/h photoperiodic rate of change concurs well with the 0·1 to 0·2 g/h figures reported for egg-type hybrids, suggesting that the photoperiodic influence on egg weight is independent of genotype.

It is likely that the significant effect of photoperiod on feed conversion efficiency was an indirect consequence of its effect on egg numbers rather than a direct effect of light on feed conversion per se. Supporting this hypothesis, there were highly significant negative regressions of both the amount of feed required to produce an egg and to produce a given weight of egg on the number of eggs laid to 68 weeks (Fig. 5). Although the elevations of these regressions depended on the growth profile during the rearing period, their slopes were not significantly different, with feed required to produce an egg decreasing by 2·3 g and the amount of feed needed to produce 1 g of egg falling by 0·025 g for each extra egg produced.

Growth

The lower feed intakes to 2·1 kg body weight of the faster-growing birds (Table 1), irrespective of photoperiod and despite them being given larger daily feed allocations, concur with the findings of Leeson & Summers (1983) that faster growing birds consume less feed to a given body weight because they have a lower total energy requirement for maintenance. Carcass analyses were not conducted in the current experiment, but it is interesting to note that Leeson and Summers (1983) found no difference in the fat and protein proportions for birds that achieved 2·1 kg at various ages between 16 and 20 weeks. The 5-week earlier age at 2·1 kg body weight in the current trial resulted in only a 10-day advance in sexual maturity, and so it is not surprising that the accelerated-growth birds were 220 g heavier than the controls at 50 % lay. Within each growth group, the variations in age at sexual maturity that had been influenced by photoperiod resulted in differences in BWSM. However, the regressions of BWSM on ASM for the two groups had significantly different slopes and elevations, with the faster-growing birds having a heavier BWSM for a given ASM, but a shallower rate of increase as ASM was delayed (Fig. 1). The findings that, for a given ASM, birds given an increased feed allocation have a heavier BWSM than conventionally managed birds concur with those of Bornstein *et al.* (1984) for two genotypes of broiler breeder given various qualitative and quantitative nutritional treatments. The findings might also support the suggestions of Dunnington *et al.* (1983) and Leeson & Summers (1983) that, in addition to thresholds for body weight and carcass composition, broiler breeders have a minimum age for gonadal development. When the effect of rate of growth on gonadal development was removed by expressing ASM relative to the age at which the birds reached 2·1 kg body weight, rather than chronologically, regressions of the lag on photoperiod showed that the faster growing groups, though maturing 10 days earlier, did not reach 50 % egg production until 25 days later than the controls (Fig. 7).

$$y = -271{\cdot}6 + 44{\cdot}72p - 1{\cdot}63p^2 + 25{\cdot}4G \quad (R^2 = 0{\cdot}948,\ P < 0{\cdot}0001,\ \text{S.D.} = 4{\cdot}32) \qquad \text{(Eqn 7)}$$

where y = lag between 2·1 kg and 50 % lay (days), p = photoperiod (h) and G = growth curve (normal = 0, accelerated = 1). In addition to the curvilinear responses showing that the groups on the more stimulatory daylengths took longer to dissipate juvenile photorefractoriness and become sexually mature, it is clear that, with the variations in age at 2·1 kg body weight removed, at least one other factor must be involved to explain the residual 25-day difference between the two groups – and this could be minimum age. Sexual maturity data from the current

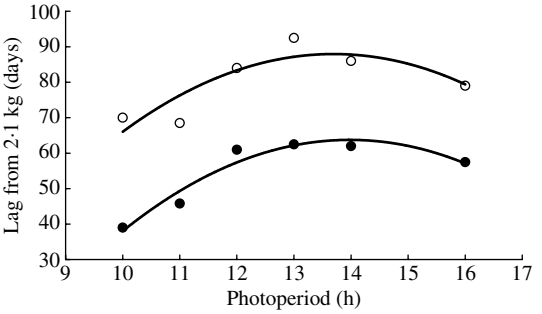

Fig. 7. Lag between ages at 2·1 kg body weight and 50 % rate of lay for Cobb 500 broiler breeder females fed to achieve 2·1 kg body weight at 17 (○) or 21 (●) weeks of age, and maintained on 10, 11, 12, 13, 14 or 16-h photoperiods.

trial (Lewis *et al.* 2004*a*) suggest a mean threshold of about 26 weeks for a flock maintained on constant photoperiods and this indicates that, with an approximate 5-week period from 0 to 50 % egg production and a 2-week requirement for rapid gonadal development, the minimum age for gonadal development for Cobb 500 pullets is about 19 weeks. This concurs well with the conclusion of Lewis *et al.* (2003) that it takes about 18 weeks for a conventionally fed flock of broiler breeders to become fully responsive to an increase in photoperiod. Although this comparison might appear inappropriate because it is of the earliest maturing birds in a flock maintained on constant photoperiods with the mean for a group given an 8-h increment in photoperiod, the figures still make sense mathematically because the 5-week difference between 0 and 50 % egg production in the current trial is cancelled out by the 5-week advance in sexual maturity observed when birds were transferred from 8 to 16 h at 18 weeks (Lewis *et al.* 2003). It must be concluded, therefore, that whatever involvement controlled feeding and photosensitivity have in the determination of sexual maturation, the mechanisms controlling body weight at, and timing of, sexual maturity are far from simple.

The increased BWSM for the accelerated growth group, compared with the controls, had no effect on egg numbers, because the 6-egg difference in egg numbers could be fully accounted for by the 10-day earlier maturity (Fig. 4). However, the similar egg production profile and increased total egg numbers for the accelerated-growth birds are in contrast to the observations of Leeson & Summers (1983) and unpublished data from an earlier trail conducted at this University that accelerating growth and advancing photostimulation results in an earlier mean ASM, lower peak rates of lay and inferior egg production to 60 weeks, despite all birds being $\geqslant$2·1 kg when photostimulated. Lewis *et al.* (2003) and other unpublished data from the University of Kwazulu-Natal

suggest that a flock of broiler breeders is unlikely to be responsive fully to an increment in photoperiod until at least 18 weeks. As a consequence, when birds are photostimulated at ages earlier than those typically used in the broiler breeding industry, the transfer to stimulatory photoperiods is likely to create a bimodal distribution of individual ages at first egg, by re-enforcing the photorefractoriness in those birds that have not yet become photoresponsive, with some birds not becoming sexually mature until almost one year of age. This lack of maturational uniformity will result in a reduced peak rate of lay and suboptimal production thereafter. In the current trial there was no photostimulation, so there would have been no bimodal distribution, and the sexual maturity of the accelerated-growth birds would have been uniformly advanced, resulting in an optimal peak and typically commercial declines in egg production thereafter. A further difference between the current findings and those reported by Leeson & Summers (1983) is that their birds, which were given up to 20% more feed and matured up to 4 weeks earlier, gained more weight after peak than controls, despite being given the same daily feed allocation in lay. Contrastingly, the accelerated-growth birds in the current trial put on significantly less body weight (820 ± 31 g) between 36 and 68 weeks than the controls (1030 ± 48 g), and ended up with a similar body weight at 68 weeks (Table 1). The complexity of the interacting responses to the growth and photoperiodic treatments is also evident in the effect that BWSM had on mean egg weight. Lewis *et al.* (1994) concluded that, irrespective of breed, it was bodyweight and not age at sexual maturity that determined egg weight in *ad libitum*-fed egg-type hybrids. Whilst egg weight also increased in proportion of BWSM for each growth group in the current trial, there were significant differences in both the slope and elevation for regressions of mean egg weight of BWSM for the two groups (Fig. 8*a*), and these are described by the following equations:

$$\text{Controls: } y = 53{\cdot}0 + 5{\cdot}31BW$$
$$(R^2 = 0{\cdot}981, P < 0{\cdot}001, \text{S.E.} = 0{\cdot}37) \qquad \text{(Eqn 8}a\text{)}$$
$$\text{Accelerated growth: } y = 41{\cdot}6 + 8{\cdot}21BW$$
$$(R^2 = 0{\cdot}904, P = 0{\cdot}004, \text{S.E.} = 1{\cdot}34) \qquad \text{(Eqn 8}b\text{)}$$

where y = mean egg weight (g) to 68 weeks, and BW = body weight (kg) at 50% egg production. These equations predict that for a given BWSM, conventionally reared birds would have a heavier mean egg weight than the birds allowed accelerated growth (Fig. 8*a*). This is in agreement with the findings of Leeson & Summers (1983), that mean egg weight to 28 weeks for birds given 1·2 times the feed allocation of controls, and which weighed 3·39 kg at 50% egg production, was more than 1 g less than controls that had a BWSM of only 3·04 kg. Whereas this suggests that growth pattern in some way affects egg weight, a stepwise regression for egg weight on BWSM, ASM, photoperiod and growth pattern eliminated growth as a significant factor ($P = 0{\cdot}772$), with the other three factors accounting for 97·0% of the variation (Eqn 6). After using the relevant coefficients to adjust the raw data to an ASM of 201·1 days (mean for this trial) and a 14-h photoperiod, the effects of BWSM were clearly linear, and, therefore, independent of growth pattern (Fig. 8*b*). The multiple regression predicted that egg weight increases by 1 g for each 380 g increase in BWSM, a rate five-times lower than the 70-g figure reported for egg-type hybrids, and, when expressed as a proportion of BWSM, egg-type hens still increased egg weight at double the rate (1 g/5·5% BWSM) of a broiler breeder (1 g/11% BWSM).

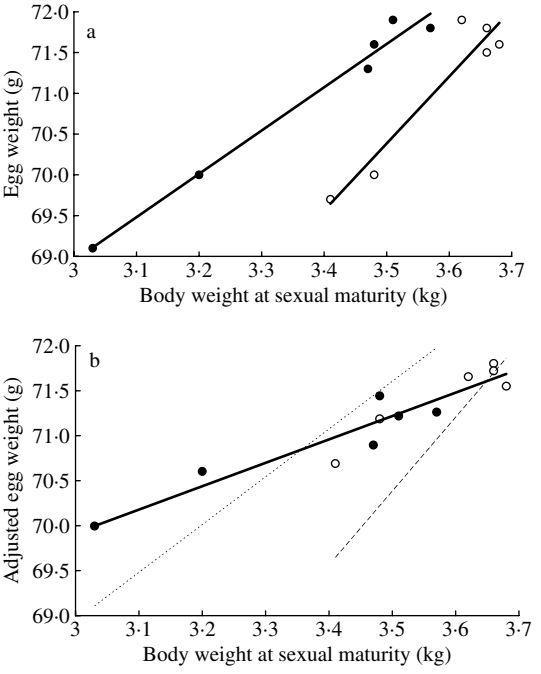

Fig. 8. (a) Mean egg weight to 68 weeks of age for Cobb 500 broiler breeder females fed to achieve 2·1 kg body weight at 17 (○) or 21 (●) weeks of age, and maintained on 10, 11, 12, 13, 14 or 16-h photoperiods, (b) Mean egg weight adjusted to a 201. 1-day sexual maturity and a 14-h photoperiod (dashed line is regression of unadjusted data for 2·1 kg body weight at 17 weeks, and dotted line is the regression of unadjusted data for 2·1 kg body weight at 21 weeks).

Notwithstanding that the overall incidence of visually abnormally large eggs was low, the significantly higher proportion for the faster-growth birds under all photoperiods (Table 3) concurs with the

many earlier reports that increasing feed allowance during rearing and accelerating growth increases the incidence of multiple follicular development (e.g. Hocking 2004).

It can be concluded that both growth pattern and constant photoperiod exert strong influences on sexual development and BWSM, and that ASM and photoperiod then significantly affect egg numbers, egg weight (together with BWSM) and feed conversion efficiency. However, it must be emphasized that the current trial studied photoperiods that were maintained throughout the life of the bird, and responses to changing photoperiods are likely to be markedly different. For example, Lewis *et al*. (2003) reported that constant 16-h birds laid 17 fewer eggs to 56 weeks than those maintained on constant 11 h, but that birds transferred from 8 to 16 h at 20 weeks laid 3 eggs more those transferred to 11 h. It is apparent, therefore, that further trials need to be conducted to establish the optimal daylength in the laying period for birds that have been reared on short days and transferred to various stimulatory photoperiods after all the birds in the group have become photoresponsive (about 18 to 20 weeks). Such lighting treatments will produce minimal differences in ASM, because the groups will be uniformly photosensitive when transferred to longer daylengths, and this will permit a better appraisal of the photoperiodic influence on rate of lay, and, additionally, its influence over the onset and persistence, or otherwise, of adult photorefractoriness.

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REFERENCES

Bornstein, S., Plavnik, I. & Lev, Y. (1984). Body weight and/or fatness as potential determinants of the onset of egg production in broiler breeder hens. *British Poultry Science* **25**, 323–341.

Dawson, A. & Goldsmith, A. R. (1983). Plasma prolactin and gonadotrophins during gonadal development and the onset of photorefractoriness in male and female starlings (*Sturnus vulgaris*) on artificial photoperiods. *Journal of Endocrinology* **97**, 253–260.

Dunnington, E. A., Siegel, P. B., Cherry, J. A. & Soller, M. (1983). Relationship of age and body weight at sexual maturity in selected lines of chickens. *Archiv fur Geflügelkunde* **47**, 85–89.

Gous, R. M. & Cherry, P. (2004). Effects of body weight at, and lighting regimen and growth curve to, 20 weeks on laying performance in broiler breeders. *British Poultry Science* **45**, 445–452.

Hocking, P. M. (1993). Effects of body weight at sexual maturity and the degree and age of restriction during rearing on the ovarian follicular hierarchy of broiler breeder females. *British Poultry Science* **34**, 793–801.

Hocking, P. M. (1996). Role of body weight and food intake after photostimulation on ovarian function at first egg in broiler breeder females. *British Poultry Science* **37**, 841–851.

Hocking, P. M. (2004). Roles of body weight and feed intake in ovarian follicular dynamics in broiler breeders at onset of lay and after a forced molt. *Poultry Science* **83**, 2044–2050.

Hocking, P. M., Bernard, R. & Robertson, G. W. (2002). Effects of low dietary protein and different allocations of food during rearing and restricted feeding after peak rate of lay on egg production, fertility and hatchability in female broiler breeders. *British Poultry Science* **43**, 94–103.

Lawes Agricultural Trust (2002). *Genstat 6th Edition, Version 6.1.0.205*. Oxford: VSN International.

Leeson, S. & Summers, J. D. (1983). Consequence of increased feed allowance for growing broiler breeder pullets as a means of stimulating early maturity. *Poultry Science* **62**, 6–11.

Lewis, P. D. (1996). The domestic hen's response to photoperiodic influences. *Proceedings XX World's Poultry Congress, New Delhi, India* **II**, 737–745.

Lewis, P. D., Backhouse, D. & Gous, R. M. (2004*a*). Constant photoperiods and sexual maturity in broiler breeder pullets. *British Poultry Science* **45**, 557–560.

Lewis, P. D., Backhouse, D. & Gous, R. M. (2004*b*). Photoperiod and oviposition time in broiler breeders. *British Poultry Science* **45**, 561–564.

Lewis, P. D., Ciacciariello, M. & Gous, R. M. (2003). Photorefractoriness in broiler breeders: sexual maturity and egg production evidence. *British Poultry Science* **44**, 634–642.

Lewis, P. D., Morris, T. R. & Perry, G. C. (1998). A model for the effect of constant photoperiods on the rate of sexual maturation in pullets. *British Poultry Science* **39**, 147–151.

Lewis, P. D., Perry, G. C. & Morris, T. R. (1994). Effect of breed, age and body weight at sexual maturity on egg weight. *British Poultry Science* **35**, 181–182.

Lewis, P. D., Perry, G. C. & Morris, T. R. (1997). Effect of size and timing of photoperiod increase on age at first egg and subsequent performance on two breeds of laying hen. *British Poultry Science* **38**, 142–150.

MacLeod, M. G., Jewitt, T. R. & Anderson, J. E. M. (1988). Energy expenditure and physical activity in domestic fowl kept on standard and interrupted lighting patterns. *British Poultry Science* **29**, 231–244.

McCluskey, W. H. & Parker, J. E. (1963). The effect of length of daily light periods on reproduction in female chickens. *Poultry Science* **42**, 1161–1165.

Morris, T. R. (1967). Light requirements of the fowl. In *Environmental Control in Poultry Production* (Ed. T. C. Carter), pp. 15–39. Edinburgh: Oliver & Boyd.

Nøddegaard, F., Talbot, R. T. & Sharp, P. J. (2000). Effect of delayed step-up lighting on plasma luteinizing hormone and reproductive function in broiler breeders. *Poultry Science* **79**, 778–783.

Robinson, J. E. & Follett, B. K. (1982). Photoperiodism in Japanese quail: the termination of seasonal breeding by photorefractoriness. *Proceedings of The Royal Society London, Series* B **215**, 95–116.

Sharp, P. J. (1988). Lighting patterns and persistency of lay. In *Science and the Poultry Industry* (Ed. J. Hardcastle), pp. 10–11. London: Agricultural and Food Research Council.

Sharp, P. J. (1993). Photoperiodic control of reproduction in the domestic hen. *Poultry Science* **72**, 897–905.

Sharp, P. J., Dunn, I. C. & Cerolini, S. (1992). Neuroendocrine control of reduced persistence of egg-laying in domestic hens: evidence for the development of photorefractoriness. *Journal of Reproduction and Fertility* **94**, 221–235.

Siopes, T. D. (2001). Temporal characteristics and incidence of photorefractoriness in turkey hens. *Poultry Science* **80**, 95–100.

Williams, J. B. & Sharp, P. J. (1978). Ovarian morphology and rates of ovarian follicular development in laying broiler breeders and commercial egg-producing hens. *British Poultry Science* **19**, 387–395.

Yu, M. W., Robinson, F. E., Charles, R. G. & Weingardt, R. (1992). Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. *Poultry Science* **71**, 1750–1761.

Yuan, T., Lien, R. J. & McDaniel, G. R. (1994). Effects of increased rearing period body weights and early photostimulation on broiler breeder egg production. *Poultry Science* **73**, 792–800.