EDUCATION AND PRODUCTION

Effects of Light Intensity from Photostimulation in Four Strains of Commercial Egg Layers: 1. Ovarian Morphology and Carcass Parameters

R. A. Renema and F. E. Robinson[1]

Department of Agricultural, Food, and Nutritional Science, University of Alberta, Edmonton, AB, Canada, T6G 2P5

ABSTRACT We examined the effects of light intensity (LI) from photostimulation to 45 wk of age on egg production parameters and egg size characteristics and on ovarian and carcass morphology at sexual maturity and 45 wk of age in four layer strains. Floor housed pullets were raised in a light-tight facility from 1 d of age until housing in individually illuminated cages at 17 wk of age. Two white egg strains, ISA-White (ISA-W) and Shaver 2000 (S2000), and two brown egg strains, ISA-Brown (ISA-B) and Shaver 579 (S579), were used. Pullets were randomly assigned to a processing group that was killed at sexual maturity (first oviposition) (Group 1) or kept to 45 wk (Group 2). Birds were photostimulated at 18 wk of age using a LI of 1, 5, 50, or 500 lx (4 × 4 factorial design). One bird from Group 1 and one from Group 2 were caged together in individually lit cages (one brown and one white egg layer). Carcass and ovarian morphology data were examined as related to Strain, LI, or the interaction of Strain and LI.

The time from photostimulation to sexual maturity did not differ due to LI, but was shorter for brown egg strains (ISA-B = 19.9 d, S579 = 20.2 d) than for white egg strains (ISA-W = 26.6 d, S2000 = 28.1 d). Body weight at sexual maturity differed among all strains, with the white egg strains having the lowest BW. Ovary weight was the greatest in ISA-W birds, in which 8.0 large yellow follicles (LYF) were present compared to 6.8 in S2000 birds. The LI affected ovary development, as birds with the 1 lx exposure had lower ovary weights and fewer LYF than did 50 lx birds, suggesting that the 1 lx LI did not result in an adequate photostimulatory cueing of sexual maturation. The threshold LI for a complete morphological response to photostimulation in this study was 5 lx. Strain differences in BW observed at sexual maturity continued to 45 wk of age. Light intensity affected 45 wk BW, with 5 lx LI birds weighing 7.2 and 8.7% more than the 50 and 500 lx birds, respectively. On an absolute basis, brown egg stains carried significantly more breast muscle at 45 wk of age than did white egg strains. The fatpad was heavier on a relative basis for brown egg layers than white egg layers. The 1 lx hens had lower 45-wk ovary weights than did the other three LI treatments. These data support the conclusion that with the development of highly specific genetic strains, it is increasingly important to match the environmental management practices to a particular hen's genotype.

(*Key words*: ovarian morphology, light intensity, strain, sexual maturation, carcass composition)

2001 Poultry Science 80:1112–1120

INTRODUCTION

The effect of light intensity (LI) on laying hens has typically been assessed through study of rate of egg production or age at first egg. Light intensities below 4 lx have been reported (Wilson et al., 1956) to delay sexual maturation of caged pullets. A 1-wk delay in sexual maturation was reported by Dorminey et al. (1970) for pullets reared under 8 h of 1.1 lx light compared to pullets reared under 3.2, 5.4, 10.8, or 32.3 lx. A dose-response increase in egg production was demonstrated by Morris (1967) for hens in three-tiered cages with LI of 0.2, 1 and 5 lx measured at the feed trough. Birds managed under 0.2 lx LI commenced lay at 9 or 12 d later than birds under 1 or 5 lx, respectively.

Morris (1994) has suggested that laying strains of the 1980s were less sensitive to light than those of the 1960s. However, when Lewis et al. (1999) compared the day of first egg data from their trial to similar treatments of Morris (1967), it was concluded that the threshold intensity required to operate the photoperiodic mechanism had not been affected by genetic selection for early sexual maturity or egg production during the period between

©2001 Poultry Science Association, Inc.

Received for publication October 16, 2000.

Accepted for publication April 9, 2001.

[1]To whom correspondence should be addressed: frank.robinson@ualberta.ca.

Abbreviation Key: D = hours of darkness; ISA-B = ISA Brown; ISA-W = ISA White; L = hours of light; LI = light intensity; S579 = Shaver 579; S2000 = Shaver 2000; LYF = large yellow follicles; POF = postovulatory follicles.

the studies. Strain differences in response to photostimulation are possible, however, as Renema et al. (2001b) found that a modern layer strain entered lay 9.1 d earlier than an antique strain when photostimulated at the same age.

There is little published data that examine the effect of LI on reproductive morphology in chickens. Robinson et al. (1998a,b) demonstrated with broiler breeders that ovarian morphology is important, as an extra large yellow follicle (LYF) at sexual maturity can be associated with a reduction in total egg production of 10.9 eggs. A recent study examining the effects of LI on sexual maturation of modern and antique laying stocks found that the ovarian morphologies of modern stocks are more affected by LI than are those of antique stocks (Renema et al., 2001b). Birds that were photostimulated with 1 lx LI had reduced ovary development and were fatter than their 50 and 500 lx counterparts. This study was the first to demonstrate an effect of LI on reproductive and carcass morphology at sexual maturity and to indicate that a LI between 1 and 5 lx is needed for a complete morphological response to photostimulation. Maximum stimulus of the photoperiodic mechanism has been proposed for LI above 5 lx, with decreasing stimulation as LI is reduced and 0.4 lx considered equivalent to darkness (Morris, 1967). Whereas the LI threshold for response is near 1 lx, Lewis and Morris (1999) stated that 5 lx is the optimum level after an integrated analysis of LI effects and economic implications.

Although there can be differences in light energy emissions of different wave lengths at a common LI, the review of Lewis and Morris (1999) does not address the use of LI over 70 to 100 lx, which can easily occur with currently used light sources, such as sodium vapor lamps. The current study was designed to compare the effects of LI on sexual maturation and egg production efficiency of white and brown egg layer strains. Particular attention was given to carcass and ovarian parameters at sexual maturity and at 45 wk of age, whereas egg production parameter data are presented elsewhere (Renema et al., 2001a).

MATERIALS AND METHODS

Stocks and Management

Four hundred eighty commercial egg-type pullets were reared following breeder guidelines in floor pens (4.75 × 5.85 m). Four strains were represented, including two white egg strains, ISA-White[2] (ISA-W) and Shaver 2000[3] (S2000), and two brown egg strains, ISA-Brown[2] (ISA-B) and Shaver 579[3] (S579). Birds from each strain were reared together until 8 wk of age, when they were subdivided into two pens (60 birds each). The birds were reared under a decreasing photoperiod in a light-tight facility with an approximate LI of 5 lx. The rearing photoperiod was 23 h of light (L):1 h of darkness (D) until 4 d of age, when the light period was shortened to 20L:4D. A further 3L were removed at 1 wk of age, followed by 2 h/wk until 5 wk of age, when a final 1 h was removed, resulting in a photoperiod of 8L:16D until 18 wk of age. This photoschedule was used to reduce or eliminate ovary and oviduct maturation prior to photostimulation. Whereas pullet growth could potentially be limited by this photoschedule, it allowed for a more precise comparison of treatments imposed at photostimulation. Feed and water were provided ad libitum. The diet schedule and the calculated nutrient analyses of the diets are presented in Table 1.

Experimental Design

At 17 wk of age, 64 pullets from each strain were individually weighed, wing-banded, and randomly placed in laying cages. Selected pullets of each strain were representative of the mean BW for that strain. A similar BW variance for each strain was observed. Pullets were assigned to one of two processing groups. Group 1 birds were killed at sexual maturity (first oviposition). Group 2 hens were kept to 45 wk. The birds were housed in standard laying cages in portable cage units with two birds per cage. Each of these two birds differed in shell color (one brown and one white egg layer) for facilitation of individual bird egg laying records. One bird from Group 1 and one bird from Group 2 were caged together. Portable cage units contained eight cages per tier with nine dimmable, overhead, incandescent bulbs located 21 cm above the dividing walls of the middle cages or the side walls of the end cages (64 cm from cage floor). Lights were cleaned, and the intensities adjusted with a quantum/radiometer/photometer[4] once per week. Light intensity was recorded at 1, 5, 50, or 500 lx, as measured at the center of the cage at approximately 22 cm above the cage floor. Further details on cage setup are provided by Renema et al. (2001b). Cages were equipped with hardware to monitor egg laying time. The resulting experimental design was a 4 × 4 factorial design (strain × LI) with 32 birds per strain and 32 birds each per LI in Groups 1 and 2 (total of 256 birds).

All birds (both groups) were photostimulated at 18 wk of age with an initial increase in photoperiod to 12L:12D and subsequent weekly light period increases of 30 min to a maximum day length of 14L:10D at 22 wk. The cage units were placed in a single, large, light-tight room divided into four quadrants by an opaque black curtain constructed to prevent light transfer between treatments while maintaining adequate ventilation (Renema et al., 2001b).

The experimental protocol was approved by the Animal Policy and Welfare Committee of the Faculty of Agriculture, Forestry and Home Economics of the University of Alberta.

[2]ISA Breeders, Inc., Box 280, Ithaca, NY 14851.
[3]Shaver Poultry Breeding Farms Limited, Cambridge, ON, Canada N1R 5V9.
[4]Model LI-188; Licor Inc., Lincoln, NE 68504.

TABLE 1. Diet schedule and nutrient analyses

Analyses	Starter 0–6 wk	Grower 1 6–12 wk	Grower 2 12–16 wk	Prelay 16–20 wk	Layer >20 wk
Calculated analysis					
Crude protein (%)	21.0	17.0	15.0	16.0	19.0
ME (kcal/kg)	2,900	2,800	2,750	2,800	2,875
Linoleic acid (%)	1.20	1.00	0.80	1.29	1.40
Methionine (%)	0.42	0.36	0.34	0.39	0.40
Lysine (%)	1.00	0.75	0.70	0.75	0.84
Calcium (%)	0.90	0.95	0.95	2.50	3.80

Carcass and Reproductive Traits

The weight of the first egg for each hen was recorded on the day of first oviposition. For Group 1 birds, after the first oviposition was recorded, feed was withdrawn overnight to facilitate gut clearance. The following morning, the bird was killed by cervical dislocation, and BW was recorded. The birds were dissected, and weights of the breast muscle, abdominal fat pad (including the fat surrounding the gizzard), oviduct, ovary, and stroma (ovary with LYF removed) were recorded.

The LYF were counted, sorted by size (with the largest follicle being the F1 follicle), and individually weighed. A follicle in the oviduct was considered the F1 follicle (most developed follicle) only prior to entry into the shell gland. An assessment of the potential for multiple ovulations to occur was determined by assigning LYF of similar size (differing by less than 1 g or 1 mm diameter) to the same position in the hierarchy as reported previously (Renema et al., 1995). Total number of positions and proportion of follicles in a multiple hierarchical arrangement were recorded. The number of complete hierarchies of LYF was calculated by dividing LYF number by the number of positions in the hierarchy (Renema et al., 1999). The number of small yellow follicles (5 to 10 mm diameter) and postovulatory follicles (POF) on the stroma were recorded. Unexplained ovulations, defined as ovulations occurring prior to first oviposition, were calculated as described by Renema et al. (1999), and calculations were adjusted for previous ovipositions and eggs in the oviduct. The carcasses were inspected for incidence of internal ovulation, internal oviposition, ovarian regression, and follicular atresia.

The Group 2 birds were processed at 45 wk of age as described above. In addition to weekly BW comparisons in these birds, the total BW gain from photostimulation to peak production (approximately 30 wk of age) and postpeak BW gain (30 to 45 wk of age) were calculated.

Statistical Analysis

The data were analyzed in a 4 × 4 factorial design. Sources of variation were strain, LI, and the interaction of strain by LI. All data were analyzed by two-way ANOVA with the general linear models procedures of SAS® software (SAS Institute, 1996). When significant differences were determined for the main effects or their interaction, comparisons among means were made using the least-significant difference procedure. For processing parameters and weekly BW, the error variation was considered to be birds within a strain and LI. Unless otherwise stated, all statements of significance were assessed using $P < 0.05$.

RESULTS AND DISCUSSION

Carcass Morphology at Sexual Maturity

The BW and composition of birds at sexual maturity was strongly affected by strain (Table 2). Mean BW of all strains differed with the brown-egg strains being the heaviest (S579 = 1,706 g; ISA-B = 1,613 g; S2000 = 1,446 g; ISA-W = 1,370 g). The relative breast muscle weight of S2000 birds at sexual maturity was 11.9% compared to a mean of 12.6% in the other strains (Table 2). Relative abdominal fatpad weight was similar in all strains, averaging 2.11% of total BW. This value was similar to those reported by Robinson et al. (1996) in pullets photostimulated at 16, 18, or 20 wk of age. Whereas relative fatpad weight was also similar to those of the modern, commercial birds of Renema et al. (2001b), they were all much lower than the 2.95% of BW reported for an antique layer strain. This finding indicates that despite differences in BW at sexual maturity, the strains tested in the current study had similar body compositions at the onset of lay.

The BW of birds within the LI treatment groups were similar at the time of photostimulation (mean of 1,363 g) (data not shown). By sexual maturity, the mean BW between LI groups approached significance ($P = 0.054$) with the 50 lx birds being slightly larger at maturity than the 5 or 500 lx birds (Table 2). The relative breast muscle and relative abdominal fatpad weights were not affected by LI at this time. Previous work has demonstrated a nonsignificant effect of LI on BW at sexual maturity (Renema et al., 2001b).

Timing of Sexual Maturity

In meat-type hens, BW is a primary determinant of the timing of sexual maturity (Hocking, 1996). In the current study, with egg-type hens, this relationship occurred to some extent. The brown egg laying strains (which were heavier than white egg laying strains) came into lay 20.1 d after photostimulation, on average, compared to 27.4 d for white egg laying strains (Table 3). There were no differences within the brown and white egg groups, however. The genetic differences associated with the brown or

TABLE 2. Body weight and breast muscle,[1] abdominal fatpad, oviduct, and ovary measurements at sexual maturity in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

Source	BW (g)	Breast muscle weight (% of BW)	Abdominal fatpad weight (% of BW)	Oviduct weight (g)	Ovary weight (g)	Stroma weight (g)
Strain[2]						
S2000	1,446[c]	11.9[b]	1.99	51.3	29.9[b]	3.17
ISA-W	1,370[d]	12.5[a]	2.10	47.9	36.8[a]	3.42
S579	1,706[a]	12.7[a]	2.37	51.4	32.3[b]	3.72
ISA-B	1,613[b]	12.6[a]	1.99	51.8	32.0[b]	3.66
SEM	17	0.1	0.13	1.3	1.4	0.22
Light intensity (lx)						
1	1,554	12.3	2.29	49.5	30.9[b]	3.37
5	1,514	12.4	1.92	50.1	32.5[ab]	3.34
50	1,560	12.3	2.14	52.3	36.1[a]	3.64
500	1,507	12.6	2.09	50.5	31.5[b]	3.61
SEM	17	0.1	0.12	1.3	1.4	0.21
	(*P*)					
Source of variation						
Strain	0.0001	0.0005	0.11	0.14	0.006	0.24
Light intensity	0.054	0.50	0.21	0.47	0.044	0.66
Strain × intensity	0.076	0.082	0.19	0.058	0.87	0.86

[a–d]Means within a column and within a source with no common superscript differ significantly ($P < 0.05$).

[1]Percentage of BW = tissue weight/BW × 100.

[2]S2000 = Shaver 2000; ISA-W = ISA White; S579 = Shaver 579; ISA-B = ISA Brown.

white egg-type birds might have been a more important determinant of the onset of lay than initial BW within the white and the brown egg-type strains. Within 5 d after photostimulation, some brown egg layers of both strains were in production, whereas the white egg strains did not have any birds in production until nearly 15 d after photostimulation (Figure 1). Brown egg layers might have been physically and physiologically more mature at photostimulation, allowing them to respond to a photostimulatory cue more quickly.

There may also be differences in their photoperiodic drive. An increased photoperiodic drive in brown com-

TABLE 3. Timing of sexual maturation, ovarian follicle numbers, unexplained postovulatory follicles (POF), and large yellow follicle (LYF) parameters at sexual maturity in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

					LYF parameters				
		Ovarian follicles[3]							
Source	Days from PS to SM[2]	LYF (n)	SYF (n)	Unexplained POF[4] (n)	Total LYF weight[5] (g)	F1 weight (g)	Number in multiple sets[6]	Percentage in multiple sets	Number of hierarchies[7]
Strain[1]									
S2000	28.1[a]	6.84[b]	5.38	0.38	21.9[b]	7.98	4.03	59.4	1.49
ISA-W	26.6[a]	8.00[a]	7.29	0.31	28.2[a]	8.04	5.42	69.3	1.59
S579	20.2[b]	7.67[ab]	6.48	0.39	25.0[ab]	7.94	4.49	61.0	1.57
ISA-B	19.9[b]	7.66[ab]	5.38	0.25	25.5[ab]	7.38	4.91	66.7	1.62
SEM	0.8	0.34	0.76	0.10	1.6	0.30	0.47	5.1	0.06
Light intensity (lx)									
1	25.4	6.79[b]	5.98	0.17[b]	23.2[b]	8.46[a]	3.71[b]	56.4	1.44[b]
5	23.0	7.44[ab]	5.91	0.16[b]	23.3[b]	7.51[b]	4.83[ab]	64.8	1.56[b]
50	23.1	8.34[a]	6.85	0.53[a]	29.2[a]	7.88[ab]	5.66[a]	71.2	1.72[a]
500	23.3	7.59[ab]	5.79	0.47[a]	24.9[b]	7.49[b]	4.66[ab]	64.1	1.55[b]
SEM	0.8	0.34	0.76	0.10	1.6	0.30	0.47	5.1	0.06
	(*P*)								
Source of variation									
Strain	0.0001	0.047	0.21	0.77	0.050	0.47	0.19	0.46	0.41
Light intensity	0.14	0.018	0.74	0.014	0.030	0.037	0.0390	0.24	0.014
Strain × intensity	0.41	0.62	0.41	0.74	0.93	0.46	0.65	0.55	0.28

[a,b]Means within a column and within a source with no common superscript differ significantly.

[1]S2000 = Shaver 2000; ISA-W = ISA White; S579 = Shaver 579; ISA-B = ISA Brown.

[2]Days from photostimulation to sexual maturity (first oviposition).

[3]LYF = >10 mm diameter; SYF = small yellow follicles (5 to 10 mm diameter).

[4]Postovulatory follicles not accounted for by eggs laid or by yolks or eggs in oviduct.

[5]LYF weight without F1 follicle.

[6]Follicles arranged in groups differing by <1 g.

[7]Hierarchies calculated as LYF divided by positions (groups of follicles within 1 g).

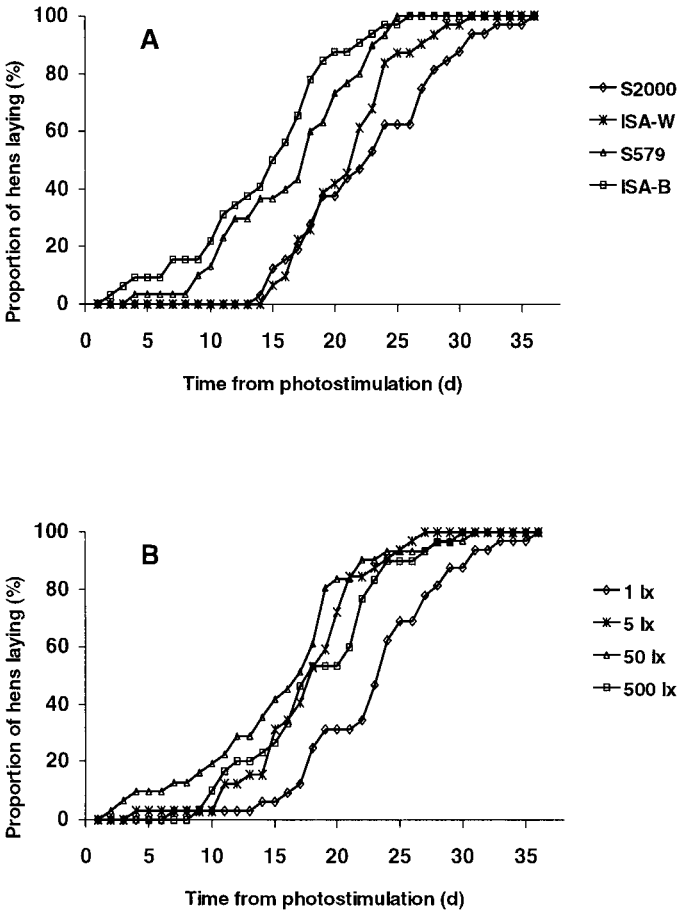

FIGURE 1. Additive curve of the proportion of pullets reaching sexual maturity for the main effect, strain (A), and light intensity (B) in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age).

pared to white egg strains would cause the brown egg strains to be more sensitive to light. Light intensity did not significantly affect the timing of sexual maturity. The apparent delay in the onset of lay in the 1 lx birds of 2.3 d (Table 3) was numerical ($P = 0.14$). This result concurs with the data of Renema et al. (2001b) and demonstrates that all intensities provided adequate light for stimulation of reproductive development. This finding also suggests that, despite rearing under a single LI, the photostimulatory effect was not due to insufficient light and darkness contrast. Meyer et al. (1988) found that a bird's photoperiodic history does not influence its likelihood of photostimulation with dim light, but photophase contrast is more critical than the absolute LI.

In their recent review of LI and performance of pullets, Lewis and Morris (1999) suggested that LI below 0.75 lx are not sexually stimulatory, whereas maximal rates of sexual maturation can be achieved with LI above 2 lx. Whereas previous studies have demonstrated a delay in the onset of lay with reduced LI (Morris, 1967; Lewis et al., 1999), these studies used three-tier battery cages with LI measurement recorded at the feed trough. In the current study, LI was measured at a constant height within the cage. Whereas all LI treatments had at least some birds in production within 10 d of photostimulation, there appeared to be a small delay in the profile of the 1 lx treatment before substantial increases in the proportion of birds in lay occurred (Figure 1B).

Ovarian Morphology at Sexual Maturity

The absolute oviduct weight was similar in all strains tested, indicating that this reproductive parameter has not been affected by genetic selection in layer stocks (Table 2). However, due to BW differences, relative oviduct weight was significantly higher in white egg strains (mean = 3.53% of BW) compared to brown egg strains (mean = 3.10% of BW) (data not shown). Oviduct weight was not significantly affected by LI (Table 2). This result differed from that of Renema et al. (2001b), who reported that a 1 lx LI did not produce the same degree of oviduct development as higher LI in Single Comb White Leghorn hens.

The ovary weight of the ISA-W birds was higher than those of all other strains on an absolute basis (Table 2) as well as on a relative basis (data not shown). Ovary weight was independent of strain-based BW effects. With the exception of the 500 lx group, ovary weight increased with LI in a dose-dependent manner (1, 5, 50, and 500 lx = 30.9, 32.5, 36.1, and 31.5 g, respectively) with the 50 lx value being significantly greater than that of the 1 and 500 lx birds (Table 2). Stroma weight was not affected by strain or LI, indicating that ovary weight differences were due to the size or number of LYF present.

The number of LYF in the ovary at sexual maturity was affected by strain, with the ISA-W hens having 8.00 LYF compared to 6.84 in S2000 hens (Table 3). Whereas the ovary weight of the S579 and ISA-B birds was lower than that of ISA-W birds, the numbers of LYF (7.67 and 7.66, respectively) were not different. Six to eight LYF are typical for high producing layer strains (Williams and Sharp, 1978). The LYF numbers related well to the total LYF weight, which was higher in ISA-W than in S2000 birds and was intermediate in the other strains. The weight of the F1 (largest) follicle did not differ between these strains, however. Apart from LYF number and weight, ovarian morphology between strains was similar. There were no strain differences in small yellow follicles number, unexplained POF, or in any of the LYF arrangement parameters (Table 3).

Light intensity caused an increase in LYF from a low of 6.79 in 1 lx birds to a high of 8.34 in 50 lx, whereas the 500 lx ovaries were intermediate with 7.59 LYF (Table 3). The number of small yellow follicles was not significantly affected by LI (mean = 6.13). Total LYF weight was greater in 50 lx birds (29.2 g) than in all other LI groups (mean = 23.8 g). The reduced quantity of LYF under low LI suggests agreement with previous observations of reduced egg production under very low LI (Morris, 1966, 1967). This observation, however, is in disagreement with Dorminey et al. (1970), Hill et al. (1988), and Tucker and Charles (1993), who reported similar rates of egg production LI ranging from 1.1 to 34 lx. Tucker and Charles

(1993) indicated that the modern, prolific, hybrid, laying hen may be more tolerant of low light intensities than earlier stocks. The current study indicates that a 1 lx LI results in reduced ovary development compared to that of birds in higher LI groups. Based on a comparison of modern and antique layer strains, Renema et al. (2001b) suggest that LI may be a more critical environmental factor with modern, highly efficient layer strains than previously thought.

The greater number of LYF at 50 lx compared to 1 lx birds also affected the arrangement of LYF on the ovary with 5.66 LYF follicles (71.2%) on 50 lx ovaries existing in pairs of similar size compared to 3.71 (56.4%) of LYF in 1 lx birds (Table 3). This phenomenon resulted in the formation of 1.72 complete hierarchies of LYF by 50 lx birds compared to 1.44 hierarchies by 1 lx birds. The percentage of LYF reported to be in a multiple hierarchical arrangement may be somewhat misleadingly for egg-type hens, as sorting of LYF into groups varying by less than 1 g may be too broad for egg-type hens. This method has been used with turkey hens (Hocking, 1992; Renema et al., 1995) and with broiler breeders (Robinson et al., 1998a; Renema et al., 1999), both of which have more and larger LYF. Laying hens typically do not suffer from as much unsettable egg production typically associated with multiple hierarchies as broiler breeders and heavy turkey breeders do, which suggests that a more narrow LYF weight range for sorting follicles into multiple sets may be more appropriate.

Interestingly, the weight of the F1 follicle was greatest in 1 lx birds (8.46 g) compared to the 5 or 500 lx birds (mean = 7.50 g) (Table 3). The total LYF weight of the 1 lx birds was very similar to that of the 5 and 500 lx birds, whereas LYF were numerically reduced by 0.65 and 0.80 compared to 5 and 500 lx birds, respectively. Within a population, birds with reduced LYF numbers generally have higher LYF weights (unpublished observation), which appeared to have occurred in the 1 lx birds. Renema et al. (2001b) found that a LI of 1 lx was insufficient for adequate ovary development. In the current study this finding is further supported by the number of unexplained POF on the ovary at sexual maturity. The 1 and 5 lx birds had an average of 0.17 unexplained POF compared to 0.50 in 50 and 500 lx birds (Table 3). Increased unexplained POF have occurred under conditions of overfeeding, when the rate of ovary development is accelerated relative to oviduct maturation rate (Melnychuk et al., 1997; Renema et al., 1999). Elevated POF in the 50 and 500 lx treatments may be indicative of an increased photostimulatory cue due to exposure to higher LI than in the other treatments. Renema et al. (2001b) reported unexplained POF values averaging 0.10 in a white egg Single Comb White Leghorn strain exposed to similar LI. The decreased ovary weight (Table 2) and numerically reduced LYF (Table 3) of the 500 lx relative to the 50 lx birds was an unexpected result, as these values have been the greatest in the 500 lx commercial layers of Renema et al. (2001b). In the current study, high LI appeared to numerically limit LYF number and size.

Carcass Morphology at 45 wk of Age

The BW of birds processed at 45 wk demonstrated that strain effects on BW at sexual maturity (Table 2) continued throughout the laying period of this study, as all strains differed from each other in the same pattern (Table 4). There were significant BW differences due to strain during every week of the breeder period (18 to 45 wk of age) (Figure 2A). All strains exhibited similar BW gains between 30 and 45 wk of age (mean BW gain = 74.0 g) (Table 4). Light intensity also affected BW at 45 wk, as the 5 lx birds weighed 7.2 and 8.7% more than did the 50 and 500 lx birds, respectively. The 1, 5, 50, and 500 lx birds gained 89, 126, 63, and 18 g between 30 and 45 wk, respectively. Examination of the BW profiles of the LI groups demonstrates that the 500 lx birds had significantly lower BW than the 1 and 5 lx birds at 22, 27, and 28 wk of age (Figure 2B). The 50 and 500 lx birds had significantly lower BW than the 5 lx birds from 36 to 38 wk of age, after which the 1 and 5 lx birds weighed more than the 500 lx birds for the duration of the experiment (Figure 2). The relationship between BW and feed intake was not studied in this trial. However, Lewis and Morris (1999) predicted, through regression analysis of six studies performed between 1946 and 1993, that daily feed intake of production hens decreases linearly by 0.2 g for each 10 lx increase in LI to 100 lx. The relationship between LI and feed intake has not been examined at higher LI, however. Skoglund et al. (1975) reported that a 5.4 lx lighting treatment resulted in a numerically higher feed intake than did 21.5 lx, 53.8 lx, or increasing lx treatments. They attributed differences in feed intake to egg production rate. In a turkey trial using LI between 54 and 324 lx, Siopes (1991) reported no differences in feed intake or feed efficiency. Abdelkarim and Biellier (1982) reported that low LI produced greater BW and egg specific gravity means than did higher LI. Increased activity and energy expenditures with higher LI have been reported by Boshouwers and Nicaise (1987).

On an absolute basis, the brown egg strains had more breast muscle at 45 wk of age than white egg strains, although on a relative basis the values were more similar (Table 4). The abdominal fatpad weight represented a higher proportion of BW in the larger strains, ranging from a high of 5.1% in S579 birds to 3.8% in ISA-B birds to a low of 3.0 in S2000 birds and 2.8% in ISA-W birds.

Absolute breast muscle weight decreased with increasing LI and represented a higher proportion of total BW in 1 lx birds compared to all other LI groups (Table 4). Whereas this may be a result of a lower rate of egg production in the 1 lx group, their relative abdominal fatpad weights were not affected. The abdominal fatpads of the 5 lx birds represented 4.4% of their BW compared to a mean of 3.4% in the other treatments.

Ovarian Morphology at 45 wk of Age

At 45 wk of age, the weight of the oviduct was lower in the ISA-W than in the S2000 and ISA-B strains (Table

TABLE 4. Postpeak BW gain and processing BW, breast muscle, abdominal fatpad, oviduct, and ovary measurements at 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

Source	Postpeak BW gain[2] (g)	BW (g)	Breast muscle		Abdominal fatpad weight (% of BW)	Oviduct weight (g)	Ovary weight (g)	Stroma weight (g)
			Weight (g)	% of BW[3]				
Strain[1]								
S2000	74.0	1,563^{c}	163.8^{b}	10.4^{b}	2.95^{c}	64.8^{a}	52.0	7.71
ISA-W	74.0	1,443^{d}	157.7^{b}	10.9^{a}	2.83^{c}	58.2^{b}	53.0	8.08
S579	73.7	1,891^{a}	198.9^{a}	10.5^{b}	5.08^{a}	62.0^{ab}	50.0	7.72
ISA-B	74.3	1,754^{b}	197.5^{a}	11.3^{a}	3.83^{b}	65.5^{a}	48.5	7.39
SEM	15.8	30	4.3	0.1	0.23	1.6	1.6	0.30
Light intensity (lx)								
1	89.2^{ab}	1,673^{ab}	188.3^{a}	11.3^{a}	3.45^{b}	63.5	45.8^{b}	7.61
5	126.2^{a}	1,745^{a}	186.7^{a}	10.7^{b}	4.36^{a}	65.4	54.5^{a}	8.17
50	63.2^{b}	1,628^{b}	173.9^{b}	10.7^{b}	3.49^{b}	59.8	52.0^{a}	7.34
500	17.5^{c}	1,605^{b}	169.1^{b}	10.5^{b}	3.40^{b}	61.7	51.2^{a}	7.51
SEM	15.8	30	4.2	0.1	0.23	1.5	1.5	0.30
	(*P*)							
Source of variation								
Strain	1.00	0.0001	0.0001	0.0003	0.0001	0.003	0.15	0.32
Light intensity	0.0001	0.005	0.002	0.002	0.006	0.056	0.001	0.21
Strain × intensity	0.98	0.98	0.65	0.15	0.63	0.51	0.11	0.61

[a–d]Means within a column and within a source with no common superscript differ significantly ($P < 0.05$).

[1]S2000 = Shaver 2000; ISA-W = ISA White; S579 = Shaver 579; ISA-B = ISA Brown.

[2]Change in BW from 30 to 45 wk of age.

[3]Percentage = tissue weight/BW × 100.

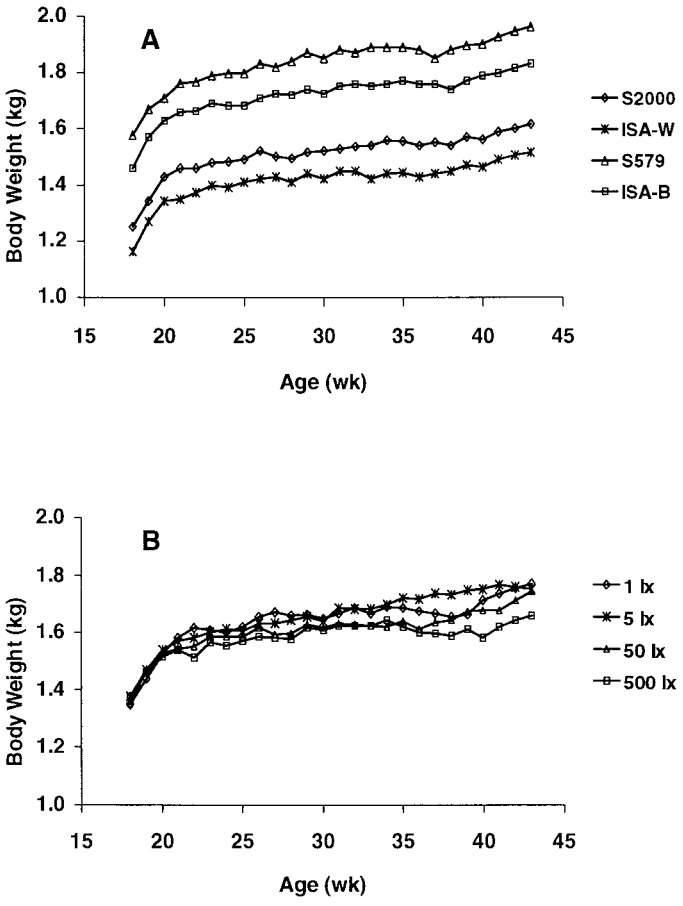

FIGURE 2. Body weight profiles for the main effect, strain (A), and light intensity (B) in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age). Significant differences occurred between all strains from 18 to 44 wk of age. Significant differences occurred between specific light intensity groups at 22, 27, and 28 wk and 36 to 44 wk of age.

4). However, ovary weight (Table 4) and the associated parameters of stroma weight (ovary without the LYF) (Table 4), ovarian follicle numbers, and LYF size and arrangement (Table 5) were not affected by strain at this time. These findings suggest that by 45 wk of age, all of the strains tested were managing their ovarian morphologies similarly. Egg production rate at this time was also similar, as indicated by hen-day production values reported for hens 38 to 45 wk of age (Renema et al., 2001a).

Light intensity did not affect oviduct weight at 45 wk of age (Table 4). However, ovary weights of the hens of the 1 lx treatment birds were less than those of all other LI groups. The mean ovary weights of the 1, 5, 50, and 500 lx birds were 45.8, 54.5, 52.0, and 51.2 g, respectively. Because ovarian stroma weight was not affected by LI (Table 4), the difference in ovary weight was presumed to be due to the weight and number of the LYF. The total weight of the LYF was higher in the 5 lx hens (34.0 g) than in the 1 lx (28.5 g) or the 500 lx (28.5 g) hens (Table 5). Ovarian LYF numbers were 5.48, 6.24, 5.71, and 5.55 in the 1, 5, 50, and 500 lx treatments, respectively, with the 5 lx birds having more LYF than the 1 and 500 lx birds. The reduced ovary size of 1 lx compared to 5 lx birds was due to fewer LYF being maintained by the ovary, which also occurred at sexual maturity (Table 3). However, in 500 lx birds, despite a similar ovary weight, the LYF number was also reduced compared to 5 lx birds. Because this reduction did not concur with data from sexual maturity, this finding may be indicative of a more rapid reproductive senescence and early onset of photorefractory conditions in the 500 lx birds. As birds age, there is an increased rate of small follicle atresia and a reduced small follicle pool size, resulting in fewer LYF in the preovulatory hierarchy (Johnson, 1993). Long-term exposure to long days is believed to accelerate the rate of

photorefractoriness in the turkey (Siopes, 1998) and the domestic hen (Sharp, 1993).

Light intensity had specific effects on LYF number within the brown egg strains. The 5 lx birds of the ISA-B strain had more LYF than did the 1 and 50 lx birds, whereas the 500 lx value was intermediate (Table 5). Within the S579 strain, the 5 lx birds had the most LYF (7.37), followed by the 50 lx birds (6.39), and the 1 and 500 lx birds were lowest with 5.50 and 5.25 LYF, respectively. Similar differences were present in the brown egg strains within the total LYF weight strain × intensity interaction. The size of LYF was also significantly affected by LI within the brown egg strains. In ISA-B birds, the F1 follicles of the 5 lx birds weighed 3.8 g more than those of 1 lx birds and 1.5 g more than those of 500 lx birds. Despite the 1 lx birds of the S579 strain having fewer LYF than 5 or 50 lx birds, their F1 weights were similar. However, the F1 follicle weight of the 500 lx birds weighed 1.9 g less, on average, than that of the other LI groups in this strain. Changes in mean LYF weight in the brown egg strains due to LI were not significance ($P = 0.078$). The LYF weight parameters of the white egg strains were affected by LI treatment even to a lesser degree than the brown egg strains. The brown egg strains had a significant strain × intensity interaction ($P = 0.009$) (Table 5). The reduced effects of LI on ovarian morphology parameters of white egg strains at 45 wk of age indicate that the ovarian morphology of these strains is less sensitive to LI effects. More substantial LI effects on these parameters may also become clearer with age.

This study demonstrated substantial differences in the sexual maturation and egg production patterns of white and brown egg laying strains. Brown egg strains reached sexual maturity approximately 1 wk earlier and at a higher BW than white egg strains. At 45 wk of age, the brown egg strains were heavier and and had more fat

TABLE 5. Ovarian follicle numbers and large yellow follicle (LYF) parameters at 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

	Ovarian follicles[2]		LYF parameters		
Source	LYF (n)	SYF (n)	Total LYF weight[3] (g)	F1 weight (g)	Mean LYF weight[3] (g)
Strain[1]					
S2000	5.79	11.9	30.9	15.5	6.47
ISA-W	5.54	14.4	30.0	15.5	6.57
S579	6.13	12.0	32.1	15.6	6.46
ISA-B	5.52	11.9	29.1	15.2	6.30
SEM	0.19	0.8	1.4	0.3	0.20
Light intensity (lx)					
1	5.48[b]	12.8	28.5[b]	15.3	6.27
5	6.24[a]	12.8	34.0[a]	16.1	6.75
50	5.71[ab]	11.8	31.1[ab]	15.3	6.58
500	5.55[b]	12.9	28.5[b]	15.0	6.20
SEM	0.19	0.8	1.4	0.3	0.20
Interaction					
S2000-1	6.00	13.1	33.0	16.4	6.62
S2000-5	5.85	12.0	32.2	15.6	6.69
S2000-50	5.57	11.6	29.8	15.3	6.56
S2000-500	5.71	11.0	28.6	14.9	6.02
ISA-W-1	5.43	14.3	30.2	15.9	6.84
ISA-W-5	5.50	12.4	30.1	15.8	6.66
ISA-W-50	5.75	15.3	30.8	14.9	6.41
ISA-W-500	5.50	15.9	28.8	15.4	6.36
S579-1	5.50[bc]	11.3	28.6[bc]	15.8[ab]	6.21
S579-5	7.37[a]	13.1	35.7[ab]	16.0[a]	6.41
S579-50	6.39[b]	10.6	38.9[a]	16.4[a]	7.30
S579-500	5.25[c]	13.0	25.1[c]	14.2[b]	5.91
ISA-B-1	5.00[b]	12.5	22.3[b]	13.3[b]	5.41
ISA-B-5	6.22[a]	13.6	37.8[a]	17.1[a]	7.24
ISA-B-50	5.14[b]	9.7	25.0[b]	14.7[ab]	6.04
ISA-B-500	5.75[ab]	11.9	31.4[ab]	15.6[a]	6.51
SEM	0.38	1.7	3.0	0.7	0.42
			(*P*)		
Source of variation					
Strain	0.11	0.062	0.50	0.78	0.81
Light intensity	0.020	0.73	0.020	0.060	0.17
Strain × intensity	0.043	0.58	0.006	0.009	0.078

[a–c]Means within a column and within a source with no common superscript differ significantly. Interaction means are compared within a strain.

[1]S2000 = Shaver 2000; ISA-W = ISA White; S579 = Shaver 579; ISA-B = ISA Brown.

[2]LYF = >10 mm diameter; SYF = small yellow follicles (5 to 10 mm diameter).

[3]LYF weight without F1 follicle.

than the white egg strains. The threshold LI for a complete morphological response to photostimulation in this study was between 1 and 5 lx. Light intensity of 1 lx limited ovary development. Body weight gain was also affected by LI, indicating the strong possibility of LI effect on feed intake. The 5 lx birds gained more weight than 50 or 500 lx birds between peak production and 45 wk of age (Table 4), had more ovarian LYF than 1 or 500 lx birds (Table 5), and had the greatest abdominal fatpad weight at the end of the trial (Table 4). Ultimately, the brown egg strains appeared to be more susceptible to the negative effects of low or high LI. Renema et al. (2001b) indicated that LI may be a more critical environmental factor with modern, highly efficient layer strains than previously thought. The current study suggests that sensitivity to LI in modern birds may vary by strain. Strain-specific management practices may become more important as genetic strains continue to become more specialized.

ACKNOWLEDGMENTS

This project was financially supported by the Alberta Agricultural Research Institute, Shaver Poultry Breeding Farms, Ltd., and ISA Breeders, Inc. Infrastructure support was provided by the University of Alberta Poultry Research Centre through funding provided by Alberta Agriculture, Food and Rural Development and the four Alberta Poultry Marketing Boards.

REFERENCES

Abdelkarim, M. R., and H. V. Biellier, 1982. Effect of light intensity and photoperiod on chicken laying hens. Poultry Sci. 61:1403–1404.

Boshouwers, F. M. G., and E. Nicaise, 1987. Physical activity and energy expenditure of laying hens as affected by light intensity. Br. Poult. Sci. 28:155–163.

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

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

Hocking, P. M., 1992. Genetic and environmental control of ovarian function in turkeys at sexual maturity. Br. Poult. Sci. 33:437–448.

Hocking, P. M., 1996. Role of body weight and food intake after photostimulation on ovarian function at first egg in broiler breeder females. Br. Poult. Sci. 37:841–851.

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

Lewis, P. D., and T. R. Morris, 1999. Light intensity and performance of domestic pullets. World's Poult. Sci. J. 55:241–250.

Lewis, P. D., T. R. Morris, and G. C. Perry, 1999. Light intensity and age at first egg in pullets. Poultry Sci. 78:1227–1231.

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

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

Morris, T. R., 1966. Light intensity for growing and laying pullets. World's Poult. Sci. J. 22:156–157.

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

Morris, T. R., 1994. Lighting for layers: What we know and what we need to know. World's Poult. Sci. J. 50:283–287.

Renema, R. A., F. E. Robinson, J. J. R. Feddes, G. M. Fasenko, and M. J. Zuidhof, 2001a. Effects of photostimulatory light intensity in four strains of commercial layers: 2. Egg production parameters. Poultry Sci. 80:1121–1131.

Renema, R. A., F. E. Robinson, V. L. Melnychuk, R. T. Hardin, L. G. Bagley, D. A. Emmerson, and J. R. Blackman, 1995. The use of feed restriction for improving reproductive traits in male-line large white turkey hens. 2. Ovary morphology and laying trait characteristics. Poultry Sci. 74:102–120.

Renema, R. A., F. E. Robinson, H. H. Oosterhoff, J. J. R. Feddes, and J. L. Wilson, 2001b. Effects of photostimulatory light intensity on ovarian morphology and carcass traits at sexual maturity in modern and antique egg-type hens. Poultry Sci. 80:47–56.

Renema, R. A., F. E. Robinson, J. A. Proudman, M. Newcombe, and R. I. McKay, 1999. Effects of body weight and feed allocation during sexual maturation in broiler breeder hens: 2. Ovarian morphology and plasma hormone profiles. Poultry Sci. 78:629–639.

Robinson, F. E., R. A. Renema, L. Bouvier, J. J. R. Feddes, J. L. Wilson, M. Newcombe, and R. I. McKay, 1998a. Effects of photostimulatory lighting and feed allocation in female boiler breeders 1. Reproductive development. Can. J. Anim. Sci. 78:603–613.

Robinson, F. E., R. A. Renema, L. Bouvier, J. J. R. Feddes, M. J. Zuidhof, J. L. Wilson, M. Newcombe, and R. I. McKay, 1998b. Effects of photostimulatory lighting and feed allocation in female boiler breeders 2. Egg and chick production. Can. J. Anim. Sci. 78:615–623.

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

SAS Institute, 1996. The SAS® System for Windows. Release 6.12. SAS Institute Inc., Cary, NC.

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

Siopes, T. D., 1998. Absence of seasonal effect on the critical day length for photorefractoriness in turkey breeder hens. Poultry Sci. 77:145–149.

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

Skoglund, W. C., D. H. Palmer, C. J. Wabeck, and J. N. Verdaris, 1975. Light intensity required for maximum egg production in hens. Poultry Sci. 54:1375–1378.

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

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

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