Effects of Light Intensity from Photostimulation in Four Strains of Commercial Egg Layers: 2. Egg Production Parameters

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ABSTRACT The effects of light intensity (LI) from photostimulation to 45 wk of age on egg production parameters and egg size characteristics were examined 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. 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 assigned to a processing group [Group 1 was killed at sexual maturity (first oviposition); Group 2 was kept to 45 wk] and 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 bird Group 2 were caged together in individually lit cages (one brown and one white egg layer). Cages were equipped with hardware to monitor egg laying time. Data of individual egg weight and time of lay were kept on Group 2 birds until 45 wk of age. Egg production data were analyzed for hen-day production, laying sequence length, egg and egg component weights, time of lay, and egg interval time as related to strain or LI.

Hen-day production was greater in brown egg strains (ISA-B = 86.7%, S579 = 88.1%) than in white egg strains (ISA-W = 83.4%, S2000 = 82.3%) and was reduced in birds under 1 lx compared to 5 or 50 lx. A LI of 1 lx resulted in reduced egg production and laying sequence length compared to birds with a 50 or 500 lx. The effects of LI were strain dependant, however. Postpeak sequence length and egg production declined at more rapidly under 500 lx compared to other LI in brown egg strains, indicating possible development of a photorefractory condition. Mean settable egg weight was lower in 500 lx birds (56.1 g) compared to other groups (mean = 57.9 g), reducing total egg mass produced. Mean interval between successive eggs in a sequence was lengthened in 1 lx birds compared to other LI groups. Mean time of lay was earlier in brown egg strains than in white egg strains by 48 min. Mean time of lay was shifted to occur later by an increasing LI.

Light intensity affected sexual maturation and egg production, as layers had differential responses to lighting. LI of 1 lx and 500 lx were found to be limiting to the egg production efficiency of layers. Whereas the birds receiving 1 lx had a reduced rate of egg production, those receiving 500 lx had reduced egg size later in the production period in combination with reduced shell quality, which indicated that inadequate feed intake under high LI conditions may be a factor affecting layer stocks. Exposure to high LI reduced egg size and total egg mass produced. Ultimately, the brown egg strains appeared to be more susceptible to the negative effects of low or high LI, indicating the importance of matching management practices to the particular hen genotype.

(*Key words*: egg layer strain, egg production, sequence length, egg weight, light intensity)

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INTRODUCTION

Selection for egg production has greatly increased ovulation frequency in commercial egg-type hens with current stocks reaching sexual maturity at earlier ages. Evidence of altered light thresholds is demonstrated by modern egg-type hens that can commence lay in the absence of photostimulatory cues (Lupicki, 1993). The extent to which light intensity (LI) influences the onset of sexual maturation and subsequent reproductive efficiency of current stocks is not well defined and research-based recommendations for commercial egg-type hen stocks are few. Meyer et al. (1988) indicated that a bird's photoperiodic history did not influence its likelihood of photostimulation with dim light but that photophase contrast was more critical than the absolute LI. An early report by

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

Roberts and Carver (1941) demonstrated no effect of LI from 9.3 to 337 lx on egg production. Morris (1966) used 25, 5, 1, and 0.2 lx and reported a logarithmic linear decline in egg production as LI decreased. King (1962) demonstrated that although pullets reared in darkness will eventually enter production, they will lay eggs at a lower rate (59% production) than that of hens raised on 6 h of light and photostimulated with 15 min weekly day-length increases (73% production).

A more recent study using caged laying hens indicated no significant effect of LI from 2 to 45 lx on egg production (Hill et al., 1988); however, the researchers suggested that the range of intensities used might not have been extreme enough to produce a clear response. Similarly, Tucker and Charles (1993) reported no significant responses to light intensities ranging from 0.5 to 15 lx, which led these authors to suggest that modern, prolific, hybrid, laying hens may be more tolerant of low LI than earlier stocks. Further support is supplied by Morris (1994), who suggested that laying strains of the 1980s were less sensitive to light than those of the 1960s. However, a study examining the effects of LI on sexual maturation of modern and antique laying stocks found that ovary development of modern stock was more limited by low LI than was antique stock (Renema et al., 2001). 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 exposed to various LI from photostimulation. In a companion paper, Renema and Robinson (2001) indicated that LI affected point-of-lay ovarian morphology in modern brown and white egg lines. This paper is a report of the egg production, laying pattern, and egg trait data from this population of hens.

MATERIALS AND METHODS

Stocks, Management, and Experimental Design

The details of the stocks used in this trial have been described elsewhere (Renema and Robinson, 2001). Briefly, 120 commercial hens of each of 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)] were reared on a decreasing photoperiod in a light-tight facility under approximately 5 lx. The photoschedule was 23 h of light (L):1 h of darkness (D) until 4 d of age and then 20L:4D (Days 4 to 7). Daylength was gradually shortened by 2 h/wk until 5 wk of age, when a final 1 h was removed, resulting in an 8L:16D photoschedule until 18 wk of age. Feed and water were provided ad libitum.

At 17 wk of age, 64 pullets from each strain were randomly selected, individually weighed, wing-banded, and housed in laying cages. Each cage held two hens, one of a brown egg strain, and the other was a white egg layer. One of the hens was designated as a Group 1 hen, which was killed at sexual maturity (first oviposition) [(data reported elsewhere (Renema and Robinson, 2001)], and the other was designated as a Group 2 hen (kept to 45 wk). At 18 wk of age, photostimulation was accomplished by an initial increase in day length to 12L:12D with subsequent weekly light period increases of 30 min to a maximum day length of 14L:10D at 22 wk. Four LI were used (1, 5, 50, or 500 lx) as measured in the center of the cage at approximately 22 cm above the cage floor. The birds were caged in standard laying cages equipped with an incandescent bulb placed over the wall between adjoining cages (for more detail, see Renema and Robinson, 2001). Cages were equipped with hardware to monitor egg laying time electronically as described by Spies et al. (2000). Briefly, an oviposition was recorded by the system if an egg interrupted the infrared beam across the egg tray. The infrared transmitter and receiver were mounted on opposite sides of the egg tray, the infrared source was pulsed every 6 s, and the pick-up signal was monitored. The cage units were placed in a large, light-tight room divided into four quadrants by an opaque black curtain constructed to prevent light transfer between treatments while maintaining adequate ventilation.

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.

Egg Production Parameters

The timing of sexual maturation was recorded for the Group 2 birds. The production of normal and defective (without a normal shell) eggs was recorded daily for each hen. Oviposition records were used to determine total and settable (marketable) egg production, the total defective eggs (double yolk, membranous, thin-shelled, abnormal shell), the mean length of laying sequences, and the length of the prime sequence. Sequences were considered to be periods of consecutive ovipositions separated by one or more pause days. The prime sequence was defined as the longest egg sequence occurring near peak egg production. Sequence lengths were determined for each hen for the entire laying period. Mean sequence length was the average length of all sequences. Weekly sequence lengths were determined by assigning each laying day a sequence length value based on the length of sequence that a bird was in on that day. Pause days (sequence = 0) were not included in the sequence analysis. For each bird, these data were summarized on a weekly basis. Hen-day egg production was calculated in a similar manner for each treatment and compared over the entire laying period as well as for early (21 to 29 wk), middle (30 to 37 wk), and late (38 to 45 wk) production. The data were analyzed to determine the interval between successive eggs within a sequence, and the mean time of oviposition.

[2]ISA Breeders, Inc., Box 280, Ithaca, NY, U.S.A. 14851.
[3]Shaver Poultry Breeding Farms Limited, Box 400, Cambridge, ON, Canada N1R 5V9.

Intervals exceeding a defined limit (32 h) were considered to be pauses and were excluded from the analysis.

All eggs laid were weighed at time of collection. The first five eggs from each Group 2 bird were broken open to determine the weight of its components (yolk, albumen, and shell). For the remainder of the laying period, two eggs were examined in this manner at 14-d intervals. Individual egg component values were calculated for the 21-to-45-wk production period by using mean values generated for each 14-d period. For each hen, weight of the first egg, mean weight of all settable eggs, and egg component weights during the early, middle, and late production period were calculated. Total egg mass was calculated as the total weight of all eggs produced. For this calculation, membranous and broken eggs were assigned the value of the mean egg weight for that bird for that week. All normal eggs produced by each bird were allocated to the appropriate Canadian egg size category [peewee (PW), <42 g; small (S), 42 to 48 g; medium (M), 49 to 55 g; large (L), 56 to 63 g; extra large (XL), 64 to 69 g; jumbo (J), > 69 g] to determine the proportion of eggs of each size.

Statistical Analysis

The experiment was analyzed as 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, comparison among means were made using the least-significant difference procedure. For overall egg production parameters, the error variation was considered to be birds within a strain and LI. For egg weight, egg component, hen-day production, sequence length, egg interval time, and mean time of lay parameters, error variation was adjusted to represent birds within a strain and LI in the comparison period (early, middle, late, or entire production period). Pearson correlation coefficients (Steel and Torrie, 1980) of the interrelationships among sequence length and laying time parameters were computed. Unless otherwise stated, all statements of significance were assessed using $P < 0.05$.

RESULTS AND DISCUSSION

Egg Production

The mean age at sexual maturity for the four strains of pullets (Table 1) were identical to that of the companion birds processed at sexual maturity (Renema and Robinson, 2001). The two white egg strains commenced lay later than the brown egg strains. Despite exposure to a similar LI during rearing, photostimulatory LI did not influence age at first egg. Meyer et al. (1988) indicated that a bird's photoperiodic history did not influence its likelihood of photostimulation with dim light but that photophase contrast was more critical than absolute LI. Total egg production to 45 wk of age was higher in the brown egg strains (S579 = 153.0; ISA-B = 150.2) than in the white egg strains (S2000 = 141.1; ISA-W = 144.3) (Table 1). Settable egg production also varied significantly due to strain, with defective egg production varying between 4.4% (S2000) and 1.9% (ISA-B). It is not known how egg production would have compared if the trial was extended beyond 45 wk of age.

A LI of 1 lx limited total egg production to 142.2 eggs compared to 148.3, 150.2, and 147.9 eggs in the 5, 50, and 500 lx treatments, respectively (Table 1). Whereas settable egg production demonstrated a similar pattern, values were statistically similar due to increased variability introduced by few birds with high levels of defective egg production. A LI of 1 lx has been suggested as the threshold for photostimulatory response in poultry, although 5 lx is believed to be the optimal minimum LI for egg production (Lewis and Morris, 1999). Hill et al. (1988) observed no significant differences in egg production with light intensities ranging from 2 to 45 lx. Contrary to the results of the current study, Tucker and Charles (1993) reported no difference in egg production when using 0.5 to 15 lx LI. Other trials have indicated that 1 lx is approximately the LI at which differences in potential or actual egg production will be expressed through delays in the onset of lay (Dorminey et al., 1970; Morris, 1967). Egg production differences in the current study were due to factors other than timing of sexual maturity, as light intensities of 1 to 500 lx caused egg production to commence at a similar age (Table 1), concurring with previous work (Renema et al., 2001). Lewis et al. (1999) provide further support by showing that the threshold intensity for stimulation of the photoperiodic mechanism was between 0.9 and 1.7 lx. This finding concurs with data from the current study.

Hen-day production for 21 to 45 wk of age was greater in the brown egg strains (88.1 and 86.7% for S579 and ISA-B, respectively) compared to white egg strains (82.3 and 83.4% for S2000 and ISA-W, respectively) (Table 1). When hen-day production was compared over three lay periods (early = 21 to 29 wk; middle = 30 to 37 wk; late = 38 to 45 wk), differences only occurred during the early period, when birds were coming into lay and reaching peak production (Table 1). Part of the superior hen-day production of the brown egg laying strains in this period can be attributed to their faster onset of lay than white egg strains. Strain effects were not significant in the middle and late periods, in which the numerical spread between the production of brown and white egg laying strains decreased to approximately 3% (Table 1).

The 1 lx birds had lower hen-day productions than the 5 or 50 lx birds for the entire 21 to 45 wk period but were not different than the 500 lx birds (Table 1). During the early production period, hen-day production increased with LI from a low of 65.7% in 1 lx birds to a high of 72.7% in 500 lx birds; 1 lx production was significantly lower than 50 or 500 lx production. During the middle period, production of all treatments was very similar. By the late period, production of the 1 and 500 lx treatments

TABLE 1. Timing of sexual maturation, total, settable and hen-day production, prime sequence length, and sequence length and profile analysis to 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

Source	Days from PS to SM[2]	Total egg production[3]	Settable egg production[2]	Hen-day production[4] Total (%) (21–45 wk)	Early (%) (21–29 wk)	Middle (%) (30–37 wk)	Late (%) (38–45 wk)	Prime sequence length (d)	Mean sequence length[5] (d)
Strain[1]									
S2000	28.0[a]	141.1[b]	134.9[c]	82.3[b]	63.9[c]	93.3	89.6	56.0[b]	20.4[b]
ISA-W	25.5[a]	144.3[b]	140.8[bc]	83.4[b]	67.8[bc]	93.8	88.5	60.3[b]	22.2[b]
S579	19.0[b]	153.0[a]	148.5[a]	88.1[a]	76.2[a]	96.4	91.7	80.5[a]	33.2[a]
ISA-B	21.9[b]	150.2[a]	147.4[ab]	86.7[a]	72.2[ab]	96.0	92.1	80.8[a]	27.9[ab]
SEM	1.0	1.7	2.7	1.0	1.6	1.8	2.0	6.3	3.5
Light intensity (lx)									
1	25.2	142.2[b]	139.3	82.5[b]	65.7[b]	93.7	87.8	55.2[b]	14.5[b]
5	22.7	148.3[a]	143.6	85.6[a]	69.8[ab]	95.1	92.7	68.4[ab]	27.7[a]
50	22.6	150.2[a]	145.2	86.9[a]	71.9[a]	95.4	93.3	79.3[a]	31.0[a]
500	23.8	147.9[a]	143.5	85.2[ab]	72.7[a]	94.8	87.9	74.7[a]	30.6[a]
SEM	1.0	1.7	2.7	1.0	1.6	1.8	1.9	6.2	3.5
	(*P*)								
Source of variation									
Strain	0.0001	0.0001	0.001	0.0001	0.0001	0.64	0.68	0.008	0.046
Light intensity	0.26	0.007	0.43	0.011	0.038	0.82	0.24	0.044	0.0001
Strain × intensity	0.51	0.11	0.23	0.15	0.78	0.53	0.13	0.61	0.32

[a–c]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]Eggs produced between sexual maturity and 45 wk of age.

[4]Hen-day production (% of flock laying/d).

[5]Mean length calculated as mean of all sequences or pauses occurring in each bird between sexual maturity and 45 wk of age.

was beginning to decline compared to the other groups, although not significantly by this point. An extension of the laying period might have shown differences that were more substantial if egg production continued to decline. Abdelkarim and Biellier (1982) found that when LI was continuously increased to a maximum or 343 to 408 lx by the eighth 28-d period of production (approximately 50 wk of age), hen-day production was increased compared to hens kept at a lower, constant LI, indicating that birds are still responsive to LI differences at the ages examined in the current study.

Sequence Length

Sequence length can be used as an indicator of the laying potential of a group of birds. High sequence lengths are associated with birds having fewer pause days and, hence, greater productivity. The mean length of all sequences was 33.2 d in S579 birds, which was higher than the 20.4 and 22.2 d for S2000 and ISA-W birds, respectively (Table 1). The ISA-B birds were intermediate with a mean length of 27.9 d. The length of the prime sequence, a characteristic long sequence occurring early in lay, averaged 80.2 d in brown egg strains compared to an average of 58.2 d in the white egg strains (Table 1). Prime sequence length can be used as an indicator of laying potential in birds managed under similar conditions because of its positive correlation with egg production totals (Robinson et al., 1990).

Near the beginning of production, when the rate of lay of all birds should be near maximum rate, the prime sequence length of 1 lx birds was 55.2 d, which was significantly lower than that of the 50 lx (79.3 d) or 500 lx (74.7 d) birds (Table 1). In our companion paper (Renema and Robinson, 2001), it was shown that the 1 lx birds had the fewest large yellow follicles (LYF) of all LI groups at sexual maturity. It is suggested that sequence length in these 1 lx birds might have been reduced due to follicular insufficiency, resulting in suboptimal production due to more pause days. Ovarian morphology at sexual maturity, particularly LYF numbers and arrangement, has been shown to have implications for long-term egg production potential (Robinson et al., 1998a,b). Fewer LYF at the onset of lay may be a consequence of altered reproductive hormone signals received by the ovary during sexual maturation (Renema et al., 1999). Renema et al. (2001) reported a 3.25 reduction in LYF in 1 lx compared to 500 lx birds at sexual maturity and anticipated that the magnitude of this difference may be great enough for long-term effects on egg production. In the current study, the mean length of all 1 lx laying sequences was 14.5 d, which was lower than that of the 5, 50, and 500 lx treatments (27.7, 31.0, and 30.6 d, respectively).

The sequence lengths suggest that egg production in the 1 lx birds began at a reduced rate compared to the other groups and that these birds were beginning to have difficulties with long-term maintenance of lay. The data shown in Figure 1 suggest a possible strain effect of LI on sequence length. The S2000 hens under all light intensities produced very similar sequence lengths; however, a declining trend in mean weekly sequence length in the 500 lx birds was apparent in the S579 and ISA-B strains, although the trial ended before significant differences in egg production were observed (Table 1). Long-term expo-

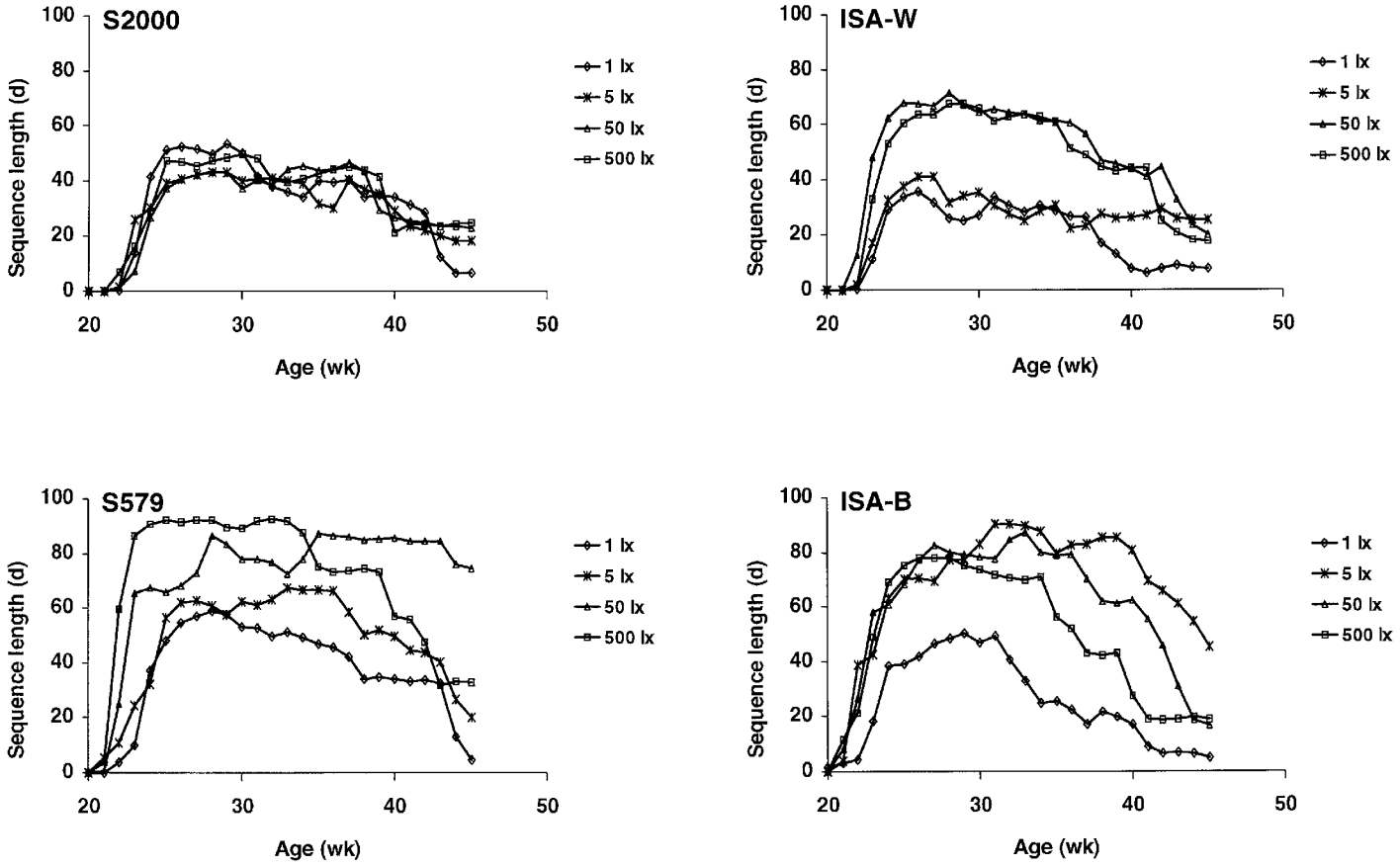

FIGURE 1. Mean weekly sequence length in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age).

sure to long days increases the rate of photorefractoriness in turkeys (Siopes, 1998) and domestic hens (Sharp, 1993). Long-term exposure to the high LI of the 500 lx treatment may accelerate reproductive senescence and early onset of photorefractoriness. Commercial lighting programs, such as the Step-Up program used in the current trial, are thought to possibly increase the rate of photorefractoriness due to early exposure to unnecessarily long days (Morris et al., 1995). However, when a similar Step-Up lighting program was tested on brown egg stocks compared to programs limiting day length during early lay, there was no difference in egg production (Morris et al., 1995). Recent work with the European Starling exposed to a photoperiod of 18L:6 D demonstrated a graded response to LI of 3, 13, 45, or 108 lx on sexual development and on the onset of photorefractoriness (Bentley et al., 1998). Whereas the 3 lx treatment slowed gonad development, the birds did not become photorefractory. The 13 lx treatment was the lowest LI to trigger a maximal rate of sexual development, whereas the onset of photorefractoriness was slowed in the 13 and 45 lx treatments compared to the 108 lx treatment. These authors suggested that there are two separate portions of the photoinducable phase—the first phase causes gonadal growth, and the second phase causes gonadal growth and photorefractoriness (Bentley et al., 1998). Longer days and higher LI are thought to initiate the second phase in the starling.

Egg Weight and Size Distribution

Mean weights of the first eggs were not affected by strain or LI (Table 2). A delayed onset of lay, as was observed for the white egg strains, would be expected to cause an increase in initial egg size. However, this relationship may be limited to specific strains, as some strains appear to have a greater emphasis on nutrient allocation to egg production than others. Despite their later onset of production, the initial egg weight of white egg strains was not different than that of the brown egg strains, possibly due in part to the lighter BW of the white egg strains at sexual maturity (Renema and Robinson, 2001).

Mean weights of settable eggs for the production period (21 to 45 wk of age) were 56.6, 56.1, 58.3, and 58.6 g for the S2000, ISA-W, S579, and ISA-B birds, respectively (Table 2). Although the eggs of the brown egg strains weighed more than those of the white egg strains in early production, this difference declined with time and was not significant in late production. In the early production period, mean egg weight of the brown egg strains was 2.7 g (5.3%) heavier than that of the white egg strains. By the middle production period, this difference had declined to 2.3 g (4.0 %) and had disappeared by late production (Table 2). Although the brown egg strains were still significantly heavier than white egg strains during late

TABLE 2. Egg weight parameters to 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

Source	Initial egg weight (g)	Mean settable egg weight: Total (g) (21–45 wk)	Early (g) (21–29 wk)	Middle (g) (30–37 wk)	Late (g) (38–45 wk)	Total egg mass[2] (kg)
Strain[1]						
S2000	41.2	56.6[b]	51.4[b]	57.6[b]	60.8	8.09[b]
ISA-W	42.6	56.1[b]	51.4[b]	57.1[b]	59.9	8.12[b]
S579	42.2	58.3[a]	54.0[a]	59.6[a]	61.3	8.83[a]
ISA-B	41.2	58.6[a]	54.2[a]	59.7[a]	61.9	8.70[a]
SEM	0.8	0.6	0.6	0.6	0.7	0.12
Light intensity (lx)						
1	42.9	58.0[a]	53.6	58.8[ab]	61.5[a]	8.26[b]
5	42.7	58.3[a]	53.0	59.3[a]	62.5[a]	8.69[a]
50	40.7	57.3[ab]	52.5	58.5[ab]	60.8[ab]	8.66[a]
500	41.2	56.1[b]	51.9	57.3[b]	59.2[b]	8.12[b]
SEM	0.8	0.6	0.6	0.6	0.7	0.12
	(*P*)					
Source of variation						
Strain	0.14	0.006	0.0001	0.005	0.25	0.0001
Light intensity	0.60	0.047	0.23	0.029	0.001	0.001
Strain × intensity	0.12	0.46	0.35	0.26	0.52	0.33

[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]Total egg mass of all eggs produced between sexual maturity and 45 wk of age.

production (Renema and Robinson, 2001), the higher BW was no longer related to a higher egg weight. Due to strain differences in egg weight, total egg mass produced also differed; the brown egg strains produced 8.77 kg of eggs, on average, compared to 8.11 kg from the white egg strains (Table 2). The allocation of eggs into the market egg size distribution was also affected by strain. The brown egg layers had a lower proportion of small- and medium-sized eggs and more eggs in the combined large, extra-large, and jumbo group (Table 3). The brown egg strains laid an average of 24.1 more eggs in the large, extra-large, and jumbo categories than the white egg strains, which may have positive revenue implications from egg sales. However, this advantage may be offset by increased feed consumption in the larger, brown egg strains.

High LI was associated with a relatively low egg weight, with the mean egg weight of 500 lx birds from 21 to 45 wk of age weighing 2.1 g less, on average, than that of the 1 and 5 lx birds (Table 2). Whereas egg weight

TABLE 3. Settable egg size distribution and value to 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

Source	Egg size distribution[2]: PW (%) (< 42 g)	S (%) (42–48 g)	M (%) (49–55 g)	L (%) (56–63 g)	XL (%) (64–69 g)	J (%) (> 69 g)	Total L, XL, and J[3]: Proportion (%)	Number
Strain[1]								
S2000	1.22	6.59[a]	29.3[a]	49.6	10.8[b]	2.54	62.9[b]	84.4[b]
ISA-W	0.91	7.12[a]	30.4[a]	52.4	8.8[b]	0.28	61.5[b]	85.8[b]
S579	0.82	4.30[b]	20.5[b]	55.3	15.7[ab]	3.25	74.3[a]	109.9[a]
ISA-B	0.75	3.47[b]	20.9[b]	52.4	20.0[a]	2.55	75.0[a]	108.5[a]
SEM	0.22	0.76	3.0	3.1	2.9	1.26	3.7	5.4
Light intensity (lx)								
1	0.53	3.62[b]	21.5[b]	58.4[a]	14.8[ab]	1.10	74.4[a]	103.2[a]
5	0.85	5.51[ab]	23.5[b]	46.6[b]	20.0[a]	3.59	70.2[a]	101.0[a]
50	1.10	5.93[a]	22.4[b]	58.1[a]	11.0[b]	1.47	70.6[a]	102.9[a]
500	1.23	6.43[a]	33.8[a]	46.5[b]	9.5[b]	2.47	58.5[b]	81.6[b]
SEM	0.22	0.76	3.0	3.1	2.9	1.26	3.7	5.4
	(*P*)							
Source of variation								
Strain	0.43	0.002	0.032	0.63	0.022	0.37	0.013	0.0003
Light intensity	0.11	0.048	0.017	0.004	0.049	0.50	0.021	0.012
Strain × intensity	0.21	0.48	0.86	0.49	0.26	0.14	0.78	0.66

[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]PW = pee-wee; S = small; M = medium; L = large; XL = extra-large; J = jumbo.

[3]Total settable egg proportion and number in the premium priced combined size category of L, XL, and J.

during the early production period did not differ significantly due to LI, it was reduced in 500 lx compared to 5 lx birds in the middle production period and compared to the 1 and 5 lx birds in the late production period. The largest spreads in egg weight were in the late period, when eggs from the 1, 5, 50, and 500 lx groups averaged 61.5, 62.5, 60.8, and 59.2 g, respectively (Table 2). At this time, the difference between 500 and 5 lx eggs reached a high of 7.1 g in the S579 strain during this period (data not shown). The weight of eggs from the 50 lx treatment did not differ from that of other LI treatments and were consistently intermediate to those of the greater and lesser light intensities, suggesting an increasingly stronger effect of higher light intensities on egg weight (Table 2). In their review of published LI data, Lewis and Morris (1999) reported a decline in mean egg weight with increasing light intensities (to a maximum of 75 lx). Their data was partly based on the results of Morris et al. (1988) and Tucker and Charles (1993), who found nonsignificant declines in egg weight with increasing LI. The ranges in LI examined in these previous studies were lower than those of the current study, however.

The negative effects of LI on egg size were clear in the comparison of egg size distributions (Table 3). The 1 lx birds produced a lower proportion of small eggs than the 50 or 500 lx groups. Medium-sized eggs were prevalent in the 500 lx group (33.8%) compared to the other LI treatments (mean of 22.5%). In the larger egg sizes, the 5 lx birds produced extra-large eggs at approximately double the rate of the 50 and 500 lx birds (Table 3). Examination of the combined total of large, extra-large, and jumbo eggs (Table 3) shows that the 1, 5, and 50 lx birds (74.4, 70.2, and 70.6%, respectively) all produced a higher total proportion of such eggs than did the 500 lx birds (58.5%). Final settable egg numbers in this premium price category were 103.2, 101.0, 102.9, and 81.6 eggs for the 1, 5, 50, and 500 lx birds, respectively (Table 3). Despite a high egg size in 1 lx birds, total egg mass output was limited due to poor egg production (Table 2). The 1 lx birds produced 8.26 kg of eggs to 45 wk of age compared to 8.69 and 8.66 kg in 5 and 50 lx birds, respectively. Whereas total egg mass of the 500 lx birds (8.12 kg) was also reduced, it was due to reduced egg size rather than rate of egg production.

Egg Components

Egg component weights among strains were primarily affected by egg weight (Table 2). Mean yolk weight for the 21-to-45-wk study period was greater in S579 eggs (14.7 g) than in S2000 eggs (14.0 g) (Table 4). Differences in yolk weights among strains changed over time. Yolk size of the brown egg strains was greater than that of the white egg strains during the early production period (Table 4), corresponding to differences in egg weight at this time (Table 2). By the late production period, when egg weight differences between strains had disappeared, yolk weights were also similar (Table 4). Egg weight was found to be correlated with absolute yolk weight ($r = 0.722$; $P = 0.0001$), whereas it was not an indicator of relative yolk weight (data not shown) ($P = 0.75$).

The 1 lx birds, which produced fewer eggs than hens of the other LI treatments (Table 1), had significantly fewer LYF than 50 lx birds at sexual maturity and had lower ovary weights than all other LI groups at 45 wk of age (Renema and Robinson, 2001), all of which likely contributed to their smaller relative yolk size. Despite a significantly reduced mean egg weight in 500 lx birds compared to 1 and 5 lx birds by late production (Table 2), yolk weight was not significantly affected by LI when examined in the three production periods (Table 4).

The mean egg specific gravity of ISA-B (1.086) was higher than that of S579 (1.083) and S2000 (1.082) eggs for the period of 21 to 45 wk of age, whereas the ISA-W value was intermediate (1.084) (Table 4). Furthermore, mean relative shell weights of eggs from ISA-B and ISA-W birds for the 21-to-45-wk period were greater than for eggs of the S579 and S2000 birds. Significant differences in egg specific gravity and shell weight occurred in the early, middle, and late production periods, with differences between strains with higher and lower relative shell weights increasing as the birds aged (Table 4). The absolute shell weights of S2000 eggs were lowest in all periods, and those of the ISA-B eggs were highest. Whereas the absolute shell weights of ISA-W and S579 eggs were similar to those of ISA-B eggs during the early period, they did not increase at the same rate as ISA-B eggs as birds aged, and they weighed significantly less during the middle and late production periods. The egg specific gravity of ISA-W eggs, which consistently had a similar relative shell weight compared to ISA-B eggs, declined at a faster rate over time (Table 4). The specific gravity of ISA-B eggs went from 1.087 in early lay to 1.085 in late lay, whereas in ISA-W eggs it decreased from 1.087 to 1.082. Eggs from ISA-B hens had higher specific gravities than eggs from all other strains in the late production period. In this study, the specific gravity of eggs was correlated with absolute shell weight ($r = 0.479$; $P = 0.0001$) and relative shell weight ($r = 0.925$; $P = 0.0001$). These relationships were consistent across all strains and light intensities. Differential changes in shell weight over time among strains suggest a strain difference in the ability to maintain calcium metabolism for optimal shell formation with age.

The absolute shell weights of 1, 5, and 50 lx eggs were greater than those of the 500 lx treatment eggs over the 21-to-45-wk production period, whereas relative shell weights did not differ (Table 4). When shell weights were compared in each production period, the 5 lx shell weights did not differ from 1 lx shells on an absolute or relative basis at any time (Table 4). However, despite similar egg sizes and shell weights, the 5 lx birds were laying at a greater rate than 1 lx birds, which might have compromised the shell quality of 5 lx eggs. The egg specific gravity of 5 lx birds during the middle production period (1.083), when birds were laying at their greatest rate, was lower than that of the 1 lx birds (1.086) (Table 4). Although the absolute shell weight of 500 lx eggs was the lowest for the 21-to-45-wk period, shell weight did

TABLE 4. Yolk weight, specific gravity, and shell weight of eggs to 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

	Yolk weight				Egg specific gravity				Absolute shell weight				Relative shell weight			
Source	Total (g) (21–45 wk)	Early (g) (21–29 wk)	Middle (g) (30–37 wk)	Late (g) (38–45 wk)	Total (21–45 wk)	Early (21–29 wk)	Middle (30–37 wk)	Late (38–45 wk)	Total (g) (21–45 wk)	Early (g) (21–29 wk)	Middle (g) (30–37 wk)	Late (g) (38–45 wk)	Total (% of egg) (38–45 wk)	Early (% of egg) (21–29 wk)	Middle (% of egg) (30–37 wk)	Late (% of egg) (38–45 wk)
Strain[1]																
S2000	**14.0**^{b}	**11.8**^{b}	**14.0**^{b}	**15.6**	**1.083**^{b}	**1.085**^{bc}	**1.083**^{b}	**1.081**^{b}	**5.38**^{c}	**5.15**^{b}	**5.39**^{c}	**5.50**^{c}	**9.43**^{b}	**9.84**^{b}	**9.45**^{b}	**9.13**^{b}
ISA-W	**14.3**^{ab}	**12.1**^{b}	**14.4**^{ab}	**15.8**	**1.084**^{ab}	**1.087**^{a}	**1.084**^{ab}	**1.082**^{b}	**5.57**^{b}	**5.44**^{a}	**5.54**^{bc}	**5.71**^{b}	**9.84**^{a}	**10.33**^{a}	**9.78**^{a}	**9.60**^{a}
S579	**14.7**^{a}	**12.9**^{a}	**14.7**^{a}	**15.8**	**1.082**^{b}	**1.084**^{c}	**1.083**^{b}	**1.081**^{b}	**5.59**^{b}	**5.48**^{a}	**5.63**^{b}	**5.62**^{bc}	**9.45**^{b}	**9.72**^{b}	**9.47**^{b}	**9.25**^{b}
ISA-B	**14.4**^{ab}	**12.8**^{a}	**14.4**^{ab}	**15.5**	**1.086**^{a}	**1.087**^{ab}	**1.086**^{a}	**1.085**^{a}	**5.82**^{a}	**5.60**^{a}	**5.82**^{a}	**5.95**^{a}	**9.84**^{a}	**10.02**^{ab}	**9.85**^{a}	**9.71**^{a}
SEM	**0.2**	**0.2**	**0.2**	**0.2**	**0.001**	**0.001**	**0.001**	**0.001**	**0.06**	**0.07**	**0.07**	**0.07**	**0.10**	**0.11**	**0.11**	**0.11**
Light intensity (lx)																
1	**14.3**	**12.4**	**14.3**	**15.6**	**1.085**^{a}	**1.087**	**1.086**^{a}	**1.084**^{a}	**5.74**^{a}	**5.55**^{a}	**5.74**^{a}	**5.86**^{a}	**9.82**	**10.12**	**9.81**	**9.61**^{a}
5	**14.6**	**12.5**	**14.5**	**16.0**	**1.083**^{b}	**1.085**	**1.083**^{b}	**1.082**^{ab}	**5.60**^{a}	**5.39**^{ab}	**5.59**^{ab}	**5.78**^{a}	**9.55**	**9.83**	**9.53**	**9.38**^{ab}
50	**14.4**	**12.5**	**14.5**	**15.7**	**1.084**^{ab}	**1.085**	**1.084**^{ab}	**1.082**^{ab}	**5.61**^{a}	**5.46**^{ab}	**5.60**^{ab}	**5.71**^{a}	**9.66**	**10.01**	**9.63**	**9.46**^{ab}
500	**14.2**	**12.2**	**14.3**	**15.4**	**1.083**^{b}	**1.086**	**1.084**^{ab}	**1.080**^{b}	**5.40**^{b}	**5.27**^{b}	**5.45**^{b}	**5.42**^{b}	**9.54**	**9.94**	**9.58**	**9.23**^{b}
SEM	**0.2**	**0.2**	**0.2**	**0.2**	**0.001**	**0.001**	**0.001**	**0.001**	**0.06**	**0.07**	**0.07**	**0.07**	**0.10**	**0.11**	**0.11**	**0.11**
	(P															
Source of variation																
Strain	0.037	0.0001	0.045	0.57	0.007	0.013	0.030	0.001	0.0001	0.0001	0.0001	0.0004	0.002	0.001	0.013	0.001
Light intensity	0.34	0.41	0.58	0.12	0.11	0.29	0.12	0.050	0.001	0.027	0.018	0.0001	0.20	0.34	0.28	0.041
Strain × intensity	0.80	0.72	0.79	0.79	0.91	0.84	0.87	0.93	0.34	0.30	0.26	0.69	0.89	0.66	0.87	0.97

[a–c]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.

TABLE 5. Laying interval and mean time of lay to 45 wk of age in four layer strains subjected to 1, 5, 50, or 500 lx by photostimulation (18 wk of age)

	Time of lay	
Source	Interval[1] (h)	Mean time[2] (h)
Strain[3]		
S2000	24.18	09:01[a]
ISA-W	24.21	09:07[a]
S579	24.18	08:04[b]
ISA-B	24.23	08:28[b]
SEM	0.05	12
Light intensity (lx)		
1	24.39[b]	07:46[c]
5	24.16[a]	08:41[b]
50	24.11[a]	08:56[ab]
500	24.17[a]	09:19[a]
SEM	0.05	12
	(*P*)	
Source of variation		
Strain	0.87	0.0008
Light intensity	0.0003	0.0001
Strain × intensity	0.15	0.99

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

[1]Interval between consecutive eggs within a sequence (pauses excluded).

[2]Mean time of lay based on a photoperiod of 14 h light:10 h darkness with lights on at 0600 h.

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

not differ in the early and middle periods (Table 4). By late production, the relative shell weights of 500 lx eggs (9.23%) were lower than those of the 1 lx eggs (9.61%). The reduced proportion of shell on 500 lx eggs in the late production period may indicate that in addition to a lower egg size at this time (Table 2), shell quality might also have been compromised. Whereas the specific gravity of 500 lx eggs did not differ from that of the lower LI during early production, by late production it was lower than that of the 1 lx birds (1.080 compared to 1.084, respectively) (Table 4). Reduced egg size and shell quality of 500 lx birds at this time may indicate insufficient feed intake in these birds compared to those of the lower LI treatments, thereby limiting intake of key minerals and vitamins for the support of shell formation.

Egg Interval and Time of Oviposition

The mean intervals between consecutive eggs within a laying sequence were similar in all strains tested, varying within 5 min (mean = 24.20 h) (Table 5). Egg interval time in broiler breeders has been reported to be 24.88 h between sexual maturity and 30 wk of age (Spies et al., 2000). Laying hens would be expected to have a shorter egg interval time because of their longer sequence lengths. In their comparison of hens selected for increased rate of lay, Naito et al. (1990) found that the reduced oviposition intervals were due to a reduced interval between oviposition and the next ovulation and to the time spent by the ovum in the shell gland.

Unlike oviposition interval time, the mean oviposition time did vary with strain. The S2000 and ISA-W hens laid their eggs at 0901 and 0907 h on average, respectively, compared to 0804 (S579) and 0828 (ISA-B) in the brown egg strains. It is not clear why this phase shift in the laying day exists between white and brown egg layers. A shorter sequence length would cause production of more first of sequence eggs, which are laid earlier in the day. Because the later-laying white egg strains had shorter sequence lengths, (Table 1), this phenomenon does not explain the differences here. Either the open period for luteinizing hormone (LH) release in the brown egg strains had shifted earlier than that of the white egg strains, or the interval between reproductive hormonal peaks in the cascade of events culminating in ovulation were shorter (reduced time to create LH surge). Lillpers (1991) observed an earlier oviposition time for the first of sequence egg from a brown egg strain than from white egg strains and hypothesized that brown egg birds had a shorter interval between the LH hormone peak and the subsequent ovulation. Lewis et al. (1995) reported this type of difference previously in their comparison of S2000 and ISA-B birds. The laying time of ISA-B hens was 1.2 to 1.4 h earlier than that of the S2000 hens using 8, 10, 13, and 18 h day lengths. As the 18-h light period also causes a shortening of the open period in ISA-B birds, they believed that the earlier eggs in ISA-B hens are due to a phase shift in the timing of the open period rather than altered timing of events surrounding the LH surge.

The mean egg interval time was similar among the 5, 50, and 500 lx groups, averaging 24.15 h (Table 5). The egg interval time for the 1 lx group was lengthened by 0.24 h relative to these groups, however. The 1 lx birds were reported to have had a significantly reduced LYF number compared to 50 lx birds at the onset of lay and at 45 wk of age (Renema and Robinson, 2001). As 1 lx birds also produced fewer eggs in total than birds in other LI treatments (Table 1), their increased egg interval may be due to fewer ovarian LYF causing larger gaps in state of maturation of the LYF present. The time increase was not due to the presence of more pause days, as pauses were removed from the analysis.

As the hens aged, the mean oviposition time shifted later in the day (data not shown). During the early period, eggs were laid at a mean time of 0824 h compared to times of 0842 and 0846 h during the middle and late production periods, respectively. Patterson (1997) found that egg production was delayed 30 to 60 min in hens at 76 compared to 36 wk of age. This change occurred independently of rate of lay, as the daily distribution of oviposition times was unaffected by rate of lay or age.

Mean time of oviposition was highly affected by LI. Eggs from 1 lx birds came earliest in the day (0746 h), followed by the 5 lx birds (0841 h), the 50 lx birds (0856 h), and finally the 500 lx birds (0919 h) (Table 5). Examination of the interaction means demonstrates that the effect of LI was very consistent in all strains tested. The early oviposition time of the 1 lx birds was initially thought to be due to increased production of first of sequence eggs

associated with their reduced sequence length compared to the other LI groups. This finding would concur with the results of Naito et al. (1989) and Lillpers (1991), who concluded that decreased mean oviposition times are due to fewer terminal eggs being produced as sequence length increased with rate of lay. Eggs produced earlier in the day have been reported to come from hens with short oviposition intervals (Lillpers and Wilhelmson, 1993). Whereas this relationship appeared to exist among the strains tested in the current study (Table 5), it does not explain the observations due to LI. Pearson correlation analysis of sequence length with mean time of lay revealed no significant relationships when performed within each strain or using all birds. In the S2000 strain, for example, there was no effect of LI on sequence length (data not shown) and yet there was a 1 h and 46 min difference in mean time of lay for the 1 and 500 lx birds of this strain. It is not clear how LI caused this phase shift in laying time. However, based on its magnitude and range, the effects of LI may be occurring through changes in the same pathways leading to the strain differences in mean time of lay. If high LI had a more stimulatory effect on reproductive processes and control pathways, oviposition time would have been expected to be advanced rather than delayed.

This study demonstrated substantial differences in the egg production characteristics of white and brown egg laying strains. Whereas the ovaries of ISA-W birds had more LYF development than the S2000 birds (Renema and Robinson, 2001), this ultimately did not affect egg production or egg weight, although shell weights were greater in the ISA-W birds. Egg production parameters were also similar between the brown egg strains, although shell weight and shell quality parameters were greater in ISA-B than in S579 birds. Whereas egg production and total egg mass of the white egg strains were reduced compared to brown egg strains, this effect may disappear when birds are kept beyond 45 wk of age. After differences in early production, egg weights of all strains became similar.

This study also demonstrated that laying strains have differential responses to lighting. One lux and 500 lx LI were found to be limiting to the production efficiency of the layer strains tested. These effects might have been exerted through altered LYF numbers (1 lx), or to reduced egg weight later in the production period (500 lx), or both. Whereas the 1 lx treatment did stimulate sexual maturation following photostimulation (Table 1), contrary to Lewis et al. (1999), it was not a full response. After an apparent inadequate photostimulation of 1 lx birds, as indicated by their significantly reduced ovary weight compared to the higher intensity groups and in LYF number compared to 50 lx birds (Renema and Robinson, 2001), there was a reduced rate of egg production in 1 lx birds (Table 1). Mean interval between successive eggs in a sequence was longer in 1 lx compared to higher LI groups. Mean time of lay was affected by strain, with brown egg strains laying 48 min earlier than white egg strains, on average. Furthermore, time of lay was shifted to a later time by an increasing LI, which could not be explained by differences in sequence length.

The threshold LI for a complete morphological response to photostimulation in this study was between 1 and 5 lx, with a 1 lx intensity resulting in inferior ovary development (Renema and Robinson, 2001) and egg production (Table 1). Body weight gain was also affected by LI (Renema and Robinson, 2001), indicating the strong possibility of a LI effect on feed intake, thereby also affecting egg production, egg size, and shell quality. Egg weight (Table 2) and shell quality (Table 4) of the low-gaining 500 lx birds (Renema and Robinson, 2001), although initially similar to that of eggs obtained under lower LI, decreased relative to that of the lower LI groups throughout the production period. High LI reduced egg size and total egg mass produced. Ultimately, the brown egg strains appeared to be more susceptible to the negative effects of low or high LI than the white egg strains. There are clearly differences in how specific strains manage egg production, which will have implications on how they are managed, as well as how they will respond to varying light intensities.

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