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I am submitting herewith a dissertation written by Hammed Akande Olanrewaju entitled "The Effects of Photoperiodism on Energy Metabolism in Broiler Chickens." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

Kelly R. Robbins, Major Professor

We have read this dissertation
and recommend its acceptance:

Karl M. Barth

Dilip L. Sachan

Michael O. Shutts

James K. Miller

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

THE EFFECTS OF PHOTOPERIODISM ON ENERGY METABOLISM IN BROILER CHICKENS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Hammed Akande Olanrewaju

May, 1990

DEDICATED TO

MY LATE FATHER

For the uncompromising principles that guided his life.

MY MOTHER

For leading her children into intellectual pursuits.

MY WIFE

For her magnificent devotion to her family

and for all those times she had to answer

a question with "He's still in school."

MY CHILDREN

For making everything worthwhile

Acnowledgements

With great indebtedness, the author wishes to acknowledge the invaluable contributions made by several important people in the preparation of this dissertation. He acknowledges with deep gratitude the constructive criticism, valuable advise, helpful suggestions, and financial assistance given in this study and round-the-clock encouragement given by my major professor, Dr. K. R. Robbins.

Appreciation is also extended to the committee members, Dr. K. M. Barth, Dr. J. K. Miller, Dr. D. S. Sachan and Dr. M. O. Smith, for their constructive criticism and assistance in the completion of this research.

The staff of the University poultry farm for the care of the chickens during the experiments.

George McGee, Eddie Jarboe, Idris Abbaker, Nikki Bell, Mary B. Davis, Mrs. Regina Robbins and her children, and others who in many diverse ways contributed to the successful completion of this work.

Last, but not least, my special gratitude to my wife, Modupeola, for her concern, love, encouragement and companionship -- the greatest incentive for going on.

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PART I

LITERATURE REVIEW

Introduction

In recent years there has been renewed emphasis on increasing the rate of protein accretion in food producing fowl. Great strides have been achieved through genetic selection, environmental control and maximizing nutritional regimes. Many avenues currently are being explored such as gene insertion and use of growth hormone. It should be emphasized that the final expression of growth and production performance are the result of interactions between nutritional, other environmental, and genetic factors with the endocrine secretions. Nutrition provides the body with its need for maintenance, growth and production. Illumination provides the bird with the needed stimulus to increase or decrease the rate of body activity and rate of growth. The body combats heat stress caused by high ambient temperatures by depressing its activities in an attempt to prevent overheating. If allowed to persist, overheating will create a physiological stress that affects growth and production negatively by promoting an unfavorable endocrine balance, by affecting metabolism or by reducing feeding intake (Hafez, 1968). Hafez (1968) also pointed out that increased physical activity, caloric intake and environmental temperature all tend to increase body temperature, but that these effects are modified by diurnal rhythms. Obviously, these interactions can be manipulated by management practices to maximize growth rate and feed efficiency and to optimize carcass characteristics. However, the considerable potential for further

stimulating growth by environmental manipulation (photoperiod) is as yet unfulfilled. The area is a focus of interest in the current years.

A somewhat new approach to this problem has been to employ compensatory growth to take advantage of an animal's capacity to maximize lean tissue development. Compensatory or "catch-up" growth is abnormally rapid growth relative to age. An enhanced rate of growth occurs when growth has been retarded either by nutritional deprivation followed by refeeding or by photoperiods. This compensatory growth has been observed in both birds and mammals, yet the reasons why this technique works have not been well explained especially the nutrition and metabolism aspects.

General View on Feeding and Lighting Programs

A number of techniques in feeding and lighting have been attempted by researchers to alleviate heat stress on poultry. Results reported in the literature are often inconsistent and sometimes contradictory. Some inconsistencies can be attributed to several factors among which are variations in breeds, housing, environment, nutrition and experimental approach.

Ermakove (1982) pointed out that discontinuous illumination promotes a more uniform distribution of the load on the digestive organs of chicks over the course of the day than constant illumination. It decreases digestive enzyme activity during the latter half of the day and therefore decreases feed nutrient utilization and rate of weight gain. Beane et al., (1979) showed that up to 6

weeks of age, birds under an intermittent lighting (IL) program were heavier than birds under a constant lighting (CL) program. They also noted that birds on ad-libitum feeding program had greater gains and better feed efficiency than birds on a restricted feeding program. Cherry et al., (1980) found that birds subjected to an IL regime were heavier and had better feed efficiency than birds on a CL regime.

Classen et al., (1989) used a commercial strain of male broiler chickens to test the effects of three lighting programs and two dietary anticoccidial agents. Low intensity incandescent light was provided on a continuous basis (24L:0D) or as one of two programs where photoperiod length was initially short and increased at different rates during the experiment. The results indicated that the two increasing lighting programs reduced 0 to 21 d body weight gain but increased 42 to 63 d gain and body weight. Moreover, incidence of mortality and skeletal disease was highest for the continuous lighting program. Broiler chicks fed on rations containing 21% protein with 2900 or 3200 Kcal ME/kg of energy were used by Diab et al., (1987) to study the effects of two lighting programs (constant light versus intermittent) and two feeding regimes (ad libitum versus restricted) up to 6 wks of age. The data indicated that broilers gained significantly more weight and had better feed efficiency under the intermittent lighting and ad-libitum feeding regimes. Moreover, the birds also performed better when fed a high energy diet, regardless of lighting or feeding regimes used. Malone et al. (1980a), who found a significant effect of lighting

lighting regimes on body weight gain, showed that birds under CL had significantly heavier body weights than those under IL, but that birds under IL had a better feed conversion rate. On the other hand, Deaton et al., (1978) found no significant differences in broiler body weight gain due to light treatment, but significant differences in feed conversion values were found to favor birds under IL over the birds under CL. Similarly, Cave, (1980) observed no differences in body weight gain among dietary treatments. Furthermore, Weaver et al., (1982) found that broilers subjected to IL in combination with increased feeding space had significantly higher body weights and better feed efficiency than birds under CL.

Feed Intake and Growth

Broiler chickens have been selected for rapid growth rate, an improvement also resulting in excess body fat. This excess carcass fat has brought about a need to better understand the nutritional, environmental, enzymatic and hormonal factors regulating lipid deposition in birds.

Increasing dietary energy concentration tends to result in a rise in energy uptake (DeGroote, 1972) and, subsequently, greater abdominal fat deposition (Elwinger, 1981). Nevertheless, it is generally considered that birds do eat to satisfy an energy requirement. Appetite for energy in excess of the requirement for maintenance/metabolism may, however, vary depending upon the number of adipocytes available for storing lipid and the efficiency of the systems involved

in lipid absorption from the intestine, lipogenesis and clearance of lipid from the plasma to adipose tissue.

Research on the restricted feeding of young chickens has been of considerable interest in recent years. Various methods of restricting feed intake of broiler chickens have been employed to improve market weight at market age, feed efficiency and reduce obesity. McDaniel et al., (1975) have shown that almost a tenth of a pound of feed can be saved per pound of broiler gain without reducing body weight by providing a 15 min feeding period followed by a 45 min period without feed each hour. The increased growth and reduced fat deposition in early-restricted compared with normal birds resulted in improvement in feed efficiency at 6 to 8 wks of age, even when considered on a body-weight basis. These results were fully confirmed under completely different conditions (Plavnik et al., 1986 and 1988). Furthermore, the reduction in deposition of carcass fat as measured 6 weeks after restriction was found to result from an inhibition of adipocyte proliferation (Cartwright et al., 1986). In contrast, Griffith et al., (1977) found that restricting the energy intake of chicks during the 0-3 wk growth period had no significant effect on fat-pad size when measured at 8 wks of age. Leveille et al., (1975) found that feed restriction for 2 h depressed hepatic lipogenesis in chicks by approximately 90% but that it was restored within 1 h of refeeding. However, March and Hansen (1977) demonstrated that restriction of nutrient intake

by dietary dilution resulted in a depression in both growth and lipid accumulation.

It has also been demonstrated that the difference in fat content between genetic lines was not due to differences in utilization of energy (Leclercq and Saadoun, 1982). Using different dietary compositions and restricted feeding for 10 days before slaughter, Arafa et al. (1983) obtained a reduction in energy intake, while the intake of protein and minerals were not below that of ad libitum feeding. An energy allowance of 90% of ad libitum intake reduced full body weight to 94% of the ad libitum fed control group; moreover, it reduced percentage of abdominal fat to 79% and slaughter weight to 95%, but there were no differences in weight of the cooked broilers.

Fraps (1943) found more that 47 years ago, that diets with a small energy to protein ratio caused less fat deposition than diets with a large energy to protein ratio. This has been confirmed more recently by several workers (Farrell et al., 1974; Jackson et al., 1982) but diets high in protein tend to be uneconomical. Cherry et al., (1984), however, did find that reduction in fat deposition as a result of feeding a diet containing a low calorie-to-protein ratio was due to a decrease in adipocyte hypertrophy rather than to any change in adipocyte number. It has been documented (Pearcel and Johnson., 1984) that feed restriction (to 70% and 60% of the ad libitum intake) significantly reduced liver weight, liver total lipid content and hepatic lipogenic enzyme specific activity but did not effect the specific activities of the glycolytic and pentose

phosphate pathway enzymes examined. McCartney and Brown, (1977) using commercial broiler male chicks to determine the effect of length of feed restriction time on growth and feed conversion, found no adverse effect on growth of broiler males by limiting the feeding time to as little as 15 min in 2 h. Furthermore, feed conversion was consistently improved by limiting feeding time. Moreover, variability in body weight was not affected until feeding time was limited to 15 min every 4 h. The weight of the digestive system was significantly larger for the birds limited in feeding time to 15 min every 4 h. The weight of the crop and proventriculus contributed the major portion to this increase while gizzard and intestine weights were not affected.

In broilers, the capacity of the gastrointestinal tract seems to be the limiting factor for ad libitum feed intake, while in layer-type birds regulation by hypothalamic hormones is more important (McCarthy and Siegel, 1983; Fisher, 1984). This is supported by the finding of Fisher and Wilson, (1974) who concluded that in 95% of the cases examined, an increase in dietary density enhanced the growth rate of broilers. Pokniak et al., (1984) has given the indication that 45% restriction in feed intake for either 14 or 28 d after hatch followed by ad libitum feeding to 56 d adversely affected growth but not feed conversion. Refeeding for both 42 or 28 d evoked a compensatory growth response, but only the 42 d refeeding period allowed the chicken to obtain an equivalent body weight when compared with the control. However, the

existence of compensatory growth in broilers remains controversial (Reid and White, 1977).

Energy Utilization

Increased heat production and metabolic rate are the major causes of poor feed utilization (Morrison and Leeson, 1978), while efficiency of feed utilization has been correlated with body growth and body weight (Proudman et al., 1970). From the report of Pym and Farrell (1977), selection for increased growth rate can be separated from selection for better feed efficiency despite the fact that the metabolic modifications associated with such responses remain unknown. Masic et al., (1974) and Barbato et al., (1980) reported that broilers consumed significantly more feed than layers, ate more meals, and spent significantly less time in feeding. Cherry and Siegel (1979) showed that feed was digested and cleared at a faster rate from a genetically-selected high body weight line of birds. This occurred even though these birds had a proportionately smaller gut. It has been proven (Marks, 1979) that as chickens age, the rate of weekly proportionate increases in body weight declines. Also, the relative amount of energy required for growth per unit metabolic body size also declines. Modern rapid-growing broilers lack well-defined appetite regulatory mechanisms (Lacy et al., 1983); consequently, modern broilers are unable to adjust energy consumption for changes in the relative requirements for growth. This may result in an increased rate of daily fat accretion.

Robbins (1981) reported that a heavy rapidly growing broiler breed was 15% more efficient in retaining ingested energy than a lighter, slower growing breed. Higher efficiency reported by Robbins (1981) may be due to a lower maintenance energy requirement, a higher efficiency of energy utilization above maintenance, or both. The report of Canolty and Koong (1976) supported this. Selection for rapid post weaning growth rate in mice resulted in a great increase in efficiency of energy utilization. Lin et al., (1979) showed that a major contributing factor to the higher energetic efficiency of genetically obese versus lean mice is a much lower maintenance requirement. Studies involving anabolic and catabolic responses to nutritional manipulation have provided valuable information regarding nutrient metabolism in chickens and other avian species. It has been shown that the difference in fat content between a genetically fat line (FL) and a genetically lean line (LL) of chickens was not due to differences in feed intake but due to differences in metabolic utilization of energy (Leclercq and Saadoun, 1982).

Photoperiod and Growth

The use of a photoperiod coupled with a controlled feeding schedule may be a possible technique for improving growth rate and feed conversion of broilers. In birds, biological rhythms readily entrained by light include body temperature, locomotor activity and feeding (Cain and Wilson, 1974; Bonita and Wayne, 1978). Therefore, a photoperiod can entrain feeding patterns

which can be manipulated by controlled feeding schedules. In addition, meal-feeding administered on a fixed daily schedule entrains peaks of activity of intestinal enzymes (Stevenson and Fierstein, 1976). Hence, timing each meal relative to periods of physical activity and to endogenous rhythms of metabolic enzymes and metabolites may be important for improved conversion of feed to animal protein.

Photoperiod, intermittent light regimes and amount of darkness per day have given inconsistent results when contrasted with continuous light or with one period of light and one period of darkness per day. Photoperiods and intermittent light regimes are reported to increase the growth rate of chicks by altering feeding behavior and increasing the efficiency of feed utilization by reducing physical activity and heat production (Ota, 1967; Osei, 1987). Favorable results have been reported by Marr et al., (1971), McDaniel (1972) and Cain (1973). Reports indicating only equal or less desirable results include Foshee et al., (1970) and Dorminey (1971). Moreover, published reports on the influence of intermittent lighting on both turkeys and market chickens have been reviewed by Buckland (1975). Cherry et al., (1978a) compared body weights and feed conversions of male broilers reared under different light regimes and fed diets containing varying nutrient densities. Broilers subjected to continuous light with alternate intervals of high- and low-density diets had significantly lower 49-day body weights when compared with broilers subjected to continuous low-intensity or intermittent light regimes. Feed conversion

comparisons followed a similar pattern. Intermittent light regimes improved neither body weight nor feed conversion when compared to continuous low-intensity illumination. Diets containing higher nutrient densities resulted in increased body weights when fed to broilers reared under continuous low-intensity light, but did not increase the performance of broilers subjected to the other light regimes. The effect of intermittent light (IL) on the growth of broilers was tested under commercial conditions by Zakaria (1987). One day old chicks were subjected to continuous light (CL) until 7 days of age and then received either CL or 7.5L:4.5D until 53 days of age. From these studies it was indicated that at 53 days of age, the mean body weight of males was greater on IL than on CL; for females, there was no difference. Follett (1981) concluded that photoperiod time measurement in Japanese quail was based on circadian rhythms which were controlled by both "dawn" and "dusk." Certainly, increased growth stimulated by intermittent light or photoperiods is dependent upon the ability of the chicken to consume large amounts of feed within a short period of time. The relationships among photoperiod, light-intensity, and the nutritive value of the diet, as well as other variables may explain the contradictory results obtained (Cherry et al., 1978b). Deaton et al., (1978) reported a significantly better feed conversion in commercial broilers reared under an intermittent lighting regime, but body weight gain was not significantly affected by light treatment. Weaver (1977) also found that feed conversion was significantly better in broilers reared under intermittent light

than by broilers reared under CL. Quarles and Kling (1974) reported that the rearing of broilers under intermittent light had no effect on carcass quality. Hooppaw and Goodman (1976) reported that chicks on intermittent light had significantly greater gains than those on continuous light. Weights of crop and gizzard contents at the end of the dark period were not significantly different among treatments; however, at the end of the light (feeding) period, chicks on intermittent light generally had significantly more feed and fluid in the crop, but not in the gizzard than chicks on continuous light.

A light control study in conjunction with feed restriction was conducted by Beane et al. (1979) with meat-type chickens. Four light treatments were utilized: CL (continuous light); 1:2 (hours light:dark); .25:1.75, and DLR (decreasing light ratio). Feed treatments were full-fed and restricted (85% of full-fed). From the study, no differences between light regimes for 8-week body weight of females were noted but the males under 1:2 were heavier than CL and DLR regimes. Broilers subjected to the restricted feed treatment exhibited considerable compensatory growth with 8-week body weights significantly reduced. Furthermore, Cherry et al., (1980) compared continuous and intermittent photoperiods of low intensity illumination with respect to their effects on the performance of commercial broilers. From their study, broilers subjected to an intermittent light regime of 1h of light and 2h darkness were significantly heavier at 56 days of age when compared to broilers receiving continuous illumination.

Thyroid Hormones and Growth

Feed intake provides substrates for growth as well as for exerting regulatory influences on the anabolic pathways involved in feed utilization. The endocrine response to feeding is a major part of this regulatory influence, with thyroid hormones playing a key role at several stages.

First, the action of insulin may be to some extent thyroid dependent, as demonstrated for glucose transport by Czech et al., (1980). A number of investigators proved beyond doubt that thyroid hormones stimulate protein synthesis in vivo at mitochondrial and nuclear levels and stimulate mitochondrial respiratory function in mammals (Katyar et al., 1977; Gordon et al., 1973). Moreover, since thyroid hormones have been reported to influence the elongation phase of protein synthesis (Mathews et al., 1973), an interaction between insulin and triiodothyronine (T_3) in the regulation of the translational phase of protein synthesis might be expected. Secondly, according to Berthoud (1984) insulin secretion is regulated in part by an adrenergic mechanism which is thyroid hormone dependent. Thus in hypothyroid animals there is reduced glucose stimulated insulin secretion due to the predominance of inhibitory α-adrenergic stimulatory responsiveness over the β-adrenegeric stimulatory responsiveness (Okajima and Ui, 1978).

Thyroid hormones are of uttermost importance for normal development and for the maintenance of a large number of processes in various tissues of the

organism. This may be a reason for the very complex regulation of the amount of thyroid hormone ultimately acting upon the cells of individual tissues. This complexity may be necessary to render possible the differential regulation of different tissues and for the detection and meeting of variations in demands due to environmental alteration, such as changes in food consumption, disease, etc. In addition, such a system has a high degree of versatility so that defects at one level can be compensated by alterations at other levels.

In the thyroid gland, the complexity is expressed by a unique type of hormone synthesis and secretion as explained by Taurog et al. (1978). First, a large "preprohormone," uniodinated thyroglobulin, is synthesized in the follicular cells. Important steps of modulation of thyroglobulin occur with formation of the iodothyromines in the peptide chains in a special extracellular compartment, the colloid, which also has a high depositing capacity for the formed "prohormone." Stimulation of the secretory processes leads to reuptake of the "prohormone" into the cells for processing by hydrolysis, which yields thyroid hormones. One of the liberated thyroid hormones, thyroxine (T_4) may also be considered to be a prohormone which in part is further processed in the thyroid as well as in peripheral tissues by deiodination in the outer ring to the active 3,5,3'-triiodothyronine (T_3), or in the inner ring to the metabolically inactive 3,3',5'-triiodothyronine (rT_3).

In recent years, broiler selection programs have placed much emphasis on rapid early growth and increased body size. Relatively little is known, however,

about the physiological mechanisms altered in the course of such genetic improvement. Bernal and DeGroote (1980), reported that although thyroid hormone might influence growth by an indirect effect involving growth hormone (GH), thyroid hormone per se has actions on growth independent of GH production. Several researchers have examined the age-related changes in thyroid hormone concentration in the chicks. May and Marks (1983) compared circulating triiodothyronine (T_3) levels in a non-selected randombred line, a commercial broiler line (growth selected) and a dwarf line (reduced growth). The broiler line had lower T_3 levels than the randombred line, and dwarf birds had significantly lower T_3 levels than either of the other lines. Both the broilers and randombred lines exhibited a peak in T_3 concentration at one week of age followed by a decline in T_3 levels to 8 weeks of age. The findings of Kuhn et al., (1982) are in agreement with this pattern of circulating T_3 levels. Kuhn et al., (1982), also reported no difference in T_3 serum level between male and female chicks although growth rate differed. Bobek et al., (1977) using white Plymouth Rock chicks observed T_3 level to increase from day 1 until 2 weeks of age and gradually decline thereafter. A major aspect of the biological role of thyroid hormones results from a primary effect on the control of gene expression (White et al., 1978).

A number of studies have examined thyroid hormones during the rapid growth phase in chickens (Stewart and Washburn, 1983; May and Marks, 1983; Thomas et al., 1986; Lilburn et al., 1986; Lauterio et al., 1986; and Goddard et

al., 1988). Most have reported an increase in plasma thyroxine with age but there are no consistent differences with ages and among strains. The age-related decrease in T_3 especially between 21 and 42 days of age has been consistently reported by the same authors for T_4 .

The relative importance of thyroxine (T_4) and triiodothyronine (T_3) as metabolically active hormones has been documented (Decuypere and Kuhu, 1984; Klandorf et al., 1978; and Sharp et al., 1984). The concentrations of the metabolically most active thyroid hormone in the blood is likely to be more closely correlated with acute changes in metabolic rate in birds than in mammals. This suggestion is supported by the observations that there are pronounced diurnal rhythms in the concentrations of plasma thyroid hormones in the chick (Newcomer, 1974; Sharp et al., 1984) but not in the rat (Fukuda et al., 1975). In general, the decrease in T_3 has been described as an adaptation in order to reduce oxygen consumption and metabolism and to preserve nutritional reserves (Tulp et al., 1979). Circadian variations of circulating T_3 and T_4 levels also have been described in birds (Harvey et al., 1980; Kuhn et al., 1982; Sharp et al., 1984; and Osei, 1987), and it seems that in the chicken the feeding pattern plays an important role in the regulation of this circadian rhythmicity (Klandorf et al., 1981). Newcomer (1974) observed that in sexually immature male chicks held on a lighting pattern of 16L:8D, the concentration of plasma T_4 increased during the dark period and decreased during the light period. Conversely, the concentration of plasma T_3 increased

during the day and fell at night. These observations suggest that the concentration of plasma T_3 is related more directly to metabolic rate than is that of T_4, since it increased during the light period when the birds would be active and decreased at night when they would be resting. Sadovsky and Bensadoun (1971) used a similar photoperiod (16L:8D) and reported that the combined concentration of T_3 plus T_4 in plasma were two times as great at 1600 than at 0400h T_3 was the predominant hormone for the times investigated. Klandorf et al., (1978) also reported that the level of T_3 fluctuated significantly in a sinusoidal wave form with maximum values occurring about 8 hours after the beginning of the light periods. The level of T_4 fluctuated significantly in a sinusoidal wave form during the 24-hour cycle but not during the 16-hour cycle. The study by Sharp et al., (1984) confirmed these reciprocal relationships between the daily rhythms in the concentration of plasma T_4 and T_3 in the chicken. These rhythms are, in part, a direct consequence of the lighting pattern since their amplitudes decrease or disappear in birds exposed to constant darkness or light for 24 hours or more. Osei (1987), reported that chickens raised under constant light had a significantly lower T_3 and T_4 concentrations than those raised under 16L:8D. Their observations are consistent with the hypothesis that T_3 is the metabolically active thyroid hormone in the chicken and T_4 secretion is stimulated by a mechanism dependent on the dark period.

Time of feeding is important in thyroid hormone rhythmicity and this is supported by report of Decuypere et al. (1984). They reported that chickens fasted during three consecutive days showed significantly lower T_3 but higher T_4 serum values compared with that of controls. The T_3 cyclicity disappeared after one day of fasting. Serum T_4 rhythmicity did not disappear, but a shift was observed in the acrophase from early morning to the late afternoon. Refeeding immediately restored the usual cycle of both T_3 and T_4. Furthermore, shifts in time of meal-eating were paralleled by shifts in circadian rhythms of glucose, rectal temperature and serum T_3 and T_4 levels. The view that the daily rhythms in levels of plasma thyroid hormones in the chicken are dependent on the pattern of feeding which in turn depends on the lighting cycle is supported by a study in broilers maintained in constant light (Sharp and Klandorf, 1984). The rhythms in levels of T_3 and T_4 were established in these birds by feeding them at the same time each day. Furthermore, the phases of the T_3 and T_4 rhythms were dependent on the time of day at which feed was available. May (1978) reported that chicken serum T_3 concentration was reduced after a 4.5-h fast, and T_4 concentration increased after a 16-h fast. Furthermore, meal feeding subsequent to a fast resulted in a T_3 concentration equal to control, full-fed chickens 2.5 hr after the meal. Chickens kept in environmental chambers at constant environmental temperature with continuous lighting and with continuous access to feed and water had no diurnal pattern for T_3 or T_4 concentration in serum. May et al., (1986) compared the relationship of

photoperiod and feed intake to thyroid hormone concentration in three trials. During the subsequent 14 days in each trial, feed was provided 12 hr/day with one chamber receiving feed during the photophase (LF) and the other during the scotophase (DF). It was observed that the weight gain of the DF broilers averaged 90% of the LF broilers for the three trials. The T_4/T_3 ratio increased during fasting and decreased when feed was available; but photoperiod had no discernable effect. The change in T_4/T_3 ratio over 24 hr was greater at high than at low environmental temperatures. Most data obtained during the scotophase involves fasting since chickens do not usually eat during the scotophase (Cherry and Barwick, 1962).

Thyroid Hormones and Skeletal Development

The actions of thyroid hormones in enhancing skeletal growth is among the most sensitive of the effects of these hormones. According to Wilkins (1965), thyroid deficiency in growing animals leads to decreased body length and delayed skeletal ossification. It has been documented by Simpson et al., (1950) and Schlesinger and Fisher (1951) that thyroid excess initially results in increased growth and accelerated skeletal maturation, which ultimately leads to decreased body length. Several in vitro studies of the effects of thyroid hormones on cartilage have failed to define clear actions on either the growth or maturation process (Audhya et al., 1975 and 1976). From the direct effect of T_3 on cartilage growth and a maturation in vitro study (Warner and Harold,

1982), it has been documented that T_3 in physiological concentrations directly affects cartilage growth and maturation, primarily through stimulating chondrocyte hypertrophy. It has been documented (Van Buul et al., 1978, 1982 and Ton and Sylvia, 1983) that partial restoration of body length, weight, and growth of several organs can be obtained by treatment with growth hormone, thyroxine and triiodothyronine. Thorngren and Hansson (1973) used daily subcutaneous injections of 5, 10, 20 or 40 μg T_4/kg. Thyroxine given in association with growth hormone had a higher growth promoting effect than either thyroxine or growth hormone alone. The width of the growth plate was not influenced by thyroxine administration. Body weight decreased somewhat when thyroxine was given alone, and the combination with growth hormone seemed to compensate for this weight loss. The effect of thyroxine on growth in length when given to hypophysectomized rats has been variable. In some studies, thyroxine has been shown to promote growth in length (Meites et al., 1964), while in other studies, this effect has not been found (Goodall and Gravin 1966).

Burch et al., (1987) reported the mechanisms by which triiodothyronine (T_3) stimulates growth and maturation of growth-plate cartilage in vitro by incubating embryonic chick pelvic cartilage in serum-free media in the presence and absence of T_3 for 3 days. The researchers proposed two different mechanisms by which T_3 affects growth-plate cartilage. First, T_3 promotes cartilage growth primarily through enhancing the effect of somotomedins.

process of cartilage differentiation from proliferative to hypertrophic chondrocytes. Thyroid hormones are essential for cartilage growth and maturation (Kan et al., 1987). In order to assess their actions during different periods of skeletal development, T_3 binding capacity in epiphyseal cartilage and T_3 concentrations in serum were quantitated in bovine fetuses of the second and third trimesters of gestation. They were then related to the alkaline phosphatase activities in the same cartilaginous tissues. From the study, T_3 binding levels which were initially low during crownrump (CR) rose to a peak value at the end of the second trimester. Then, following a sharp decline at 50-60 cm CR, T_3 binding rose to a moderate level in the later gestational period (60-90 cm CR). Hypophysectomy in the growing chick was followed by reduced body and skeletal (shank-toe length) growth (Scanes et al., 1986). In addition, decreases were observed in tibia length and weight, the plasma concentrations of immunoreactive-somatomedins C(IR-SMC), free fatty acids and weight for the heart, liver, pectoralis, thymus and bursa fabricus. Body and skeletal growth were increased by the administration of T_3. T_3 also increased tibia weight and length and returned the proximal growth plate thickness to that found in intact controls. Similarly, T_3 administration was followed by increases in the weights of the heart, liver, thymus and bursa fabricius.

Thyroid Hormones and Lipogenesis

Thakare (1987), observed that malic enzyme activity in the soluble fraction of the neonatal brain of hypothyroid rats was lowered as compared to that of the control animals. Administration of T_3 to neonates of control animals resulted in significant enhancement in the activity of malic enzyme. The study indicated that brain malic enzyme is involved in lipogenesis; hence myelination responds to T_3 in the early stage of life. Recordings of rats' diurnal ad libitum feeding patterns and responses to short term feed deprivation (Le-Magnen, 1988), suggested that analysis of diurnal feeding rhythms could provide a clue for understanding mechanisms involved in control and regulation of feed intake. Negative correlations between nocturnal lipogenesis and subsequent daytime lipolysis and the diurnal cycle of free fed rats compared to hibernators provides evidence on the nature of the lipostatic mechanism and its monitoring by hypothalamic ventromedial nuclei. It has been previously reported (Levacher et al., 1984) that in the rat, chronic thyroxine (T_4) treatment includes a transient adipose tissue hyperplasia and that, in preadipocyte cultures, lipogenesis as well as adipose conversion were enhanced by triiodothyronine (T_3). The same authors (Levacher et al., 1988) looked for the possibility of a relationship between in vivo stimulation of adipose tissue lipogenesis and the stimulation of fat cell recruitment by thyroid hormones. They estimated hepatic and adipose tissue de novo lipogenesis by the incorporation of ^3H_2O into lipids in rats of

various ages made slightly hyperthyroid by daily injections of T_4 from birth. Hepatic and adipose tissue lipogenesis were increased at 3 and 6 weeks of age and no stimulation was observed when animals aged. At 21 weeks, animals were acutely treated with 0.2 or 2 micrograms T_4/g/day; only the high T_4 dose was able to consistently stimulate lipogenesis in liver and in adipose tissue. The authors pointed out that thyroid hormones can stimulate lipogenesis both in liver and adipose tissue. However, there is an age related fall in the sensitivity to thyroid hormone for lipogenesis stimulation, not only in the liver but also more pronounced in adipose tissue. Moreover, this decreased sensitivity seems to be accelerated by a long lasting hyperthyroidal state. In keeping with this decreased response to thyroid hormones with age, it may be recalled that carbohydrate inducible levels of lipogenic enzymes are decreased with age in adipose tissue (Kaiser et al., 1983) and that triiodothyronine was said to be a multiplier of carbohydrate-generated signals responsible for the induction of malic enzyme formation in vivo (Mariash et al., 1981) and in vitro (Mariash et al., 1981).

Energy Nutrition and Metabolism

Chicks differ from rats in the relative contribution of adipose tissue and liver to lipogenesis. While in the rat adipose tissue constitutes the main site of fatty acid synthesis, in the chick the contribution of this tissue is negligible and the liver is the main site of this process. Another difference between these

species is in the relation between the rate of fatty acid synthesis and the activity of lipogenic enzymes.

The relationships among glucose tolerance, insulin secretion and fat deposition in the domestic chicken are not clear, probably because a specific assay for avian insulin was only recently developed (McMurtry et al., 1983). Avian species are strikingly resistant to large doses of insulin as well as to diabetogenic techniques. Simon (1980) was unable to relate differences in fat deposition to glucose tolerance responses in meat-type chickens. However, Sorenson (1971) reported differences in plasma insulin and glucose concentrations between two experimental lines of chickens differing in adiposity. In the chicken, as in mammals, glucose exhibits large individual variation, is insulin-dependent, and is modified by factors such as fasting (Simon et al., 1978) and intermittent feeding (Simon et al., 1979). Simon et al. (1982) reported that plasma glucose level in a high abdominal fat line (HL) was lower than in the low line (LL) but there were no differences in plasma insulin concentrations. During refeeding following a fast, plasma glucose levels were similar in both lines. Nancy et al., (1987) reported that low body weight (LW) chicks were better able to clear glucose from their blood than were their high body weight (HW) counterparts, and the FI crosses (HL) exhibited intermediate responses. Osei (1987) reported that light significantly depressed liver lipogenesis, jejunal glucose uptake, and T_3 and T_4 concentrations. Thus, gluconeogenesis appeared likely not only to be responsible for the blood glucose

increase but also to play a role in the restoration of liver glycogen after initial glycogenolysis due to fasting.

Circadian rhythms in various metabolic systems have been noted in many species for numerous biological parameters (Mills, 1966), but very few studies on diurnal variations in the chicken have been conducted. Pauly and Schening (1967) found that blood glucose levels were higher in nocturnal laboratory rats during hours of darkness than during hours of light on a schedule of 12h light and 12h darkness. Gilbert et al. (1970) reported similar results in broiler chickens. The blood glucose levels of young chickens were sampled during alternating periods of darkness and light and a significant difference between the blood glucose levels of birds sampled during hours of darkness and light was found.

Twiest and Smith (1970) reported that ad libitum fed chickens maintained on a 12:12 light-dark schedule exhibited a significantly higher blood glucose level just before the start of the light period and during the lighted hours than during the dark hours. In contrast to this, Krishan (1973) indicated that no diurnal variation existed in plasma glucose, triglyceride, insulin or in liver glycogen concentrations when young and old chicks were fed and bled at 6-h intervals throughout 24-h. From the same studies, plasma glucose, cholesterol and triglyceride values seem to be age dependent and were lower in the older birds. Furthermore, March (1984) reported that following a 16-h fast, plasma glucose was higher in broiler-type chicks whereas plasma triglyceride

concentrations were higher in White Leghorn chicks. It was concluded that feeding pattern seems to control the diurnal variations in the chicks and that these variations were diet dependent rather than light cycle dependent.

Due to the limited capacity to store polysaccharides, glucose ingested in excess of immediate energy needs and storage capacity is converted by glycolysis into pyruvate and then acetyl-CoA from which fatty acids are synthesized. In fowl, the liver is the primary site of fatty acid synthesis (Leveille et al., 1968 and O'Hea et al., 1968). It has been shown that in vivo lipogenesis and activities of lipogenic enzymes in chickens and quail are affected by biotin status, dietary fat, starvation and dietary levels of mercury and selenium. It was recently found that light-breed chicks could be easily overfed but heavy-breed chicks could not (Nir et al., 1978). Shapira et al. (1978) overfed chicks of a heavy breed (HB) and a light breed (LB) for 18 days while the activities of some enzymes involved in lipogenesis in the liver and adipose of overfed and ad lib-fed chicks were determined. Ad lib-fed HB chicks consumed more feed, gained more weight and deposited more fat than the corresponding LB chicks. Lipogenic enzymes in both adipose tissue and liver were more active in Hb than in the LB chicks. Overfeeding increased the weight and fat content of liver and adipose tissue in both breeds. The specific activities in liver and adipose tissue increased in ad lib-fed chicks in which the increase was derived mainly from tissue enlargement. They concluded that lipogenic enzymes of chicks respond to an increased substrate flux. It was

suggested that the enlarged liver, the higher participation of adipose tissue in lipogenesis and the uninterrupted supply of crop-stored excess feed enable the chick to accommodate the increased amount of substrate with only moderate enzymic adaptation. The increase in the hepatic lipogenic enzyme activities during prolonged overfeeding roughly paralleled the metabolic energy intake expressed on a per unit metabolic weight basis.

Fat is stored as triglycerides in fat cells. In contrast to mammals, avian fat cells cannot synthesize triglycerides, but have only storage function (Evans, 1977). The triglycerides are transported by the blood and are derived directly from the feed, or from the liver and to a lesser extent from the skeleton where the triglycerides are synthesized from fatty acids (Nir et al., 1982). Net change in the amount of stored triglyceride of adipose tissue clearly depends on the balance between the process of synthesis and storage, and the opposing process of mobilization of fat. Siegel (1981) and Calabotta et al. (1983) compared lipogenic and lipolytic capacities of adult male chicks from two divergent lines developed through selection for body weight at 8 weeks of age. Their results indicated that, at least in mature males, lipid turnover differed between these lines. In comparison to the high-weight males, those from the low-weight line exhibited higher activities of lipogenic enzymes, increased in vitro mobilization of free fatty acids (FFA) from adipose tissue, and higher concentrations of FFA in plasma. The high-weight males, in contrast, appeared to synthesize fat at a slower rate, but a corresponding decrease in lipolytic rate prevented a net loss

in fat stores. Calabotta et al., (1983 and 1985) examined lipogenic and lipolytic capacities in fasted and nonfasted 28 day-old chicks from high-weight and low-weight selected lines. Their results pointed out that fasting depressed lipogenesis and increased lipolysis. Regardless of the feeding state, low-weight chicks exhibited higher lipogenic and lipolytic capacities than their high-weight counterparts. Saadoun (1984) compared liver and adipose tissue in vivo lipogenesis in genetically lean or fat male chickens using tritiated water. It was observed that fatty acid synthesis was more pronounced in liver than in other tissues in both lines, while liver synthesis was 26% higher in fat birds than in lean. Moreover, the livers of fat chickens were heavier than those of lean chickens and this difference was partly due to the triglyceride content of the livers of fat-line birds. In the fasting or fed state, fat line (FL) chickens showed a higher plasma concentration of triglycerides and triglyceride-rich lipoproteins than lean line (LL) chickens (Hermier et al., 1984). This finding strongly suggests that hepatic synthesis and/or secretion of triglycerides was more active in the FL than in the LL birds. Direct evidence of a hypersecretion of triglycerides from the liver of the FL chickens, as compared to the LL ones, has been shown from recent in vivo tracer experiments with ^{14}C-acetate (Legrand et al., 1987).

It has been shown that the rate of lipogenesis is markedly reduced by fasting and is restored to normal or greater than normal levels upon refeeding in rats (Masoro et al., 1962; Jansen et al., 1967). Similar effects of fasting and

refeeding on lipogenesis have been observed in chicken livers (Leveille, 1969; Goodridge, 1968). The consequences of fasting and refeeding on the activity of several lipogenic enzymes have also been studied in rats and chicks. In rats, the activities of hepatic hexose monophosphate shunt dehydrogenases, malic enzyme and citrate cleavage enzyme were reduced by fasting and returned to above normal levels upon refeeding (Kornacker et al., 1965). In chicks, the activities of malic enzyme, citrate cleavage enzyme and glucose-6-phosphate dehydrogenase were altered in a parallel fashion with lipogenesis by fasting and refeeding (Leveille, 1969; Goodridge, 1968). The changes in lipogenesis discussed above were observed within a period of 24 to 72 hours of fasting and similar periods of refeeding.

Yeh et al., (1970) reported an "overshoot" in hepatic lipogenesis induced by longer periods of refeeding. The specific activities of malic enzyme and citrate cleavage enzyme were not altered by the short periods of fasting or refeeding studied. The marked depression in hepatic lipogenesis resulting from a short period of fasting was closely related to increased levels of plasma free fatty acids. The level of circulating free fatty acids increased with time of fasting and returned to normal upon refeeding.

Later work by Tanaka et al., (1983a, 1983b) seemed to indicate that both dietary protein and fat were antilipogenic even when fed in conjunction with a constant quantity of carbohydrate calories. In contrast, the work of Hillard et al, (1980) indicated that dietary fat per se did not inhibit de novo lipogenesis

in birds. Interpretation of the effects of energy sources on lipogenesis (Donaldson, 1985) is difficult because the usual method of adding fat to chick diets, isocaloric substitution of fat for corn meal, also results in a decrease in the carbohydrate level of the resultant diet. It has been documented (Rosebrough et al., 1987) that an increase in dietary protein (23 versus 13%) increased in vitro glucose production in chicks. In contrast, the same increase in dietary protein decreased in vitro lipogenesis in the liver. Moreover, the same increase in dietary protein increased both insulin and thyroxine (T_4) and decreased triiodothyronine (T_3) concentrations. Serum T_3 and T_4 concentrations were less and insulin concentrations were greater in 4-wk old chicks compared to 2-wk old chicks.

Plasma free fatty acids (PFFA), which usually account for about 5% of total plasma lipids, are of major metabolic importance in both mammals and avians. Studies in many animals have confirmed that plasma FFA concentrations are low in fed animals (0.2-0.3 mmol/L) and raised (0.5 to 1.5 mmol/L) during starvation.

As shown by several researchers, the regulation of lipolysis in avian adipose tissue in vitro and probably in vivo differs markedly from that of most mammals studied. Reports from Langslow and Hales (1969) and Goodridge (1968a) are pertinent to this topic. Langslow et al., (1969) reported that catecholamines are considered to be of minor importance in regulation of avian lipolysis and free fatty acid mobilization. Rather, investigations imply that

glucagon is the prime lipolytic hormone in birds (Grande, 1968; Grande et al., 1970). No effect was observed in vivo either to the cateholamines or in vitro to porcine ACTH (Langslow and Hales, 1969). While the spontaneous lipolytic rate in adipose tissue obtained from fasted pigeons was increased concomitant with depressed oxygen consumption, addition of epinephrine did not alter activity of the tissue (Goodridge et al., 1967). That the pattern of response of avian adipose tissue differs from that of other experimental animals is indicated further by data indicating a remarkable sensitivity of intact chicken adipose tissue and isolated fat cells to glycogen-induced lipolysis, a sensitivity which is further enhanced by addition of insulin (Langslow and Hales, 1969). Glucagon elevated avian plasma free fatty acids when given to intact birds (Langslow et al., 1970), and stimulated mobilization of FFA from chicken adipose tissue in vitro (Langslow and Hales, 1969).

The results of these and other studies indicate that the presence of a photoperiod is necessary for normal growth and development of broiler chicks. However, the effects of constant light versus a photoperiod on nutrient metabolism and growth are not well understood. Furthermore, it is apparent that dramatic changes in the partitioning of nutrients occur at some point during and prior to compensatory growth. Factors which facilitate a state of accelerated tissue deposition are not understood. Hence, additional information is needed. In view of these facts, these studies were undertaken to investigate the role of photoperiod in body growth and metabolism. Various experiments

were carried out to find out how photoperiod and nutrients influence body weight and several metabolic parameters associated with growth and energetic efficiency.

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PART II

EFFECTS OF LIGHT TREATMENT, SEX, AND DIET ON GROWTH OF BROILER CHICKENS.

Abstract

The effects of sex, light treatment (16L:8D versus constant light), and dietary energy and their interactions on growth performance of broiler chickens were evaluated. The diets used were isonitrogenous (23% CP); the dietary energy concentration was either 3300 kcal ME/kg diet or 2475 kcal ME/kg diet. The results indicated that light treatment had significant effects on weight gain, feed consumption, and gain/feed ratio. Constant light depressed growth after the third week of age in each trial. Birds reared under a 16L:8D photoperiod and fed a high energy diet performed best. Within light treatment, males gained more, consumed more feed, and had a higher feed efficiency than females. The light treatment x dietary energy concentration interaction was found to be significant for feed consumption and gain/feed ratio. It was concluded that combining a photoperiod of 16L:8D with high dietary energy under either an ad-libitum or restricted feeding regime resulted in a substantial and significant improvement in overall performance of broiler chickens.

Introduction

In recent years, broiler chickens have been selected for rapid growth rate, but the improvement in growth has also resulted in excess body fat. Recently, there has been an increased public awareness of the possible health problems associated with an excessive consumption of fat. In broiler chickens, while subcutaneous fat is associated with finish and eating qualities, excess fat

accumulation is undesirable both from the producer and consumer standpoint. This consideration is important because of the research implicating excess dietary fat in the human diet and cardiovascular disease. In addition, adiposity that exceeds normal requirements for thermoregulation and energy storage can adversely affect many aspects of commercial poultry production, processing waste management, by-product composition and especially consumer acceptance (Heath et al., 1980). The leaf fat attached to broiler backs poses a labor problem since it must be removed by hand prior to mechanical deboning and before the water used in processing is released into the environment. Currently, losses due to excess fat deposition in broiler chickens are estimated at $250-300 million annually (Rosebrough et al., 1986).

It has been indicated that fat metabolism in the modern broiler can be controlled somewhat if the bird is subjected to some form of energy restriction in the early growth period (Plavnik et al., 1985). It is common practice to restrict feed intake of broiler chickens to produce leaner carcasses at market age. This is beneficial not only from the standpoint of producing a healthier bird but also in reducing feed costs during the rearing period. Energy restriction has been shown to result in a reduction in metabolic energy loss (Mitchell, 1962) leading to a reduced requirement for maintenance. Research has shown that there may be an advantage in restricting feed intake to 75 to 85% of the amount of feed that would be consumed on a free choice basis (Rosebrough et al., 1986) with compensatory growth after 21 days in a

restriction-refeeding system. The capacity of an animal to overcome such nutritional deprivation is well-documented. However, the effects of feed restriction on metabolism have received little attention despite the practical interest in restricting energy intake in domestic fowl especially. Alterations and biological signals which occur during and prior to compensatory growth and which facilitate a state of accelerated tissue deposition are not understood and require further investigation.

Some commercial broilers are now being reared under photoperiodic housing systems (Weaver, 1977) with different photoperiods and intermittent light under moderate temperature conditions. It has been reported that a rearing program restricting day length significantly reduced the fat content of turkeys (Anonymous, 1985). Es Van (1981) found that intermittent light gave less fat deposition. Bonita et al. (1978) and Deaton et al.(1978) could find no significant effect of lighting systems on total carcass or abdominal fat. Results of these and other studies indicate that the presence of a photoperiod is necessary for normal growth and development of broiler chicks.

The objectives of this study were to determine the effects of sex, photoperiod, and energy restriction and their interactions on growth, feed intake and efficiency of broiler chickens.

Materials and Methods

Shaver Color-Pac sexed broiler chicks were used in two experiments. Fertile eggs were obtained from breeder flocks maintained at the University of Tennessee and hatched at the University hatchery. One day posthatching, chicks were sexed and all morbid, unthrifty chicks were discarded. The remaining chicks were individually wingbanded and randomly distributed to treatment groups.

Chickens were housed in electrically heated battery brooders kept in light-proof, heated, and ventilated rooms. In one room, lights remained on 24 hours per day. In the other room a 16 hour light:8 hour dark photoperiod was imposed. Light intensity at bird level measured 14.5 lux. The temperature of both rooms, monitored twice daily, did not on any day differ between rooms by more than 1°C and averaged 28°C throughout the experimental periods. The chickens were housed in electrically-heated battery-brooders through 4 weeks of age, then transferred to unheated grower batteries for the remaining 3 weeks. All chicks were started in the appropriate photoperiod at 1 or 5 days posthatching. Each experiment lasted 4 to 7 weeks.

In experiment 1, feed and water were provided ad libitum. A soybean meal based semi-purified diet was used. All experimental diets were formulated to be isonitrogenous (23% CP) and contained either 3300 kcal ME/kg or 2475 kcal ME/kg diet as shown in Table 1. All other

TABLE 1

Composition of the experimental diets

Basal Diet	#1[1] (%)	#2[2] (%)
Dextrose	15.00	15.00
Soybean Meal (47.47% CP[3])	48.35	48.35
Corn starch	9.75	10.80
Soy oil	13.87	4.06
Salt premix[4]	5.37	5.37
Vitamin premix[5]	0.20	0.20
Choline chloride	0.40	0.40
DL - methionine	0.23	0.23
Cellulose	6.83	15.59
	100.00	100.00

[1] -High energy diet was formulated to contain 23% CP; 3300 Kcal ME/kg.

[2] -Low energy diet was formulated to contain 23% CP; 2475 Kcal ME/kg.

[3] -As analyzed

[4] -provided per kg diet: $CaCO^3$ 3g; $Ca^3(PO_4)_2$, 28g; K_2HPO_4 9g; NaCl, 8.8g; $MgSO_4.7H_2O$, 3.5g; $MnSO_4.H_2O$, .65g; Ferric citrate, 5g; $ZnCO_3$, .1g; $CuSO_4.5H_2O$, 0.02g; $Na_2MoO_4.2H_2O$, .001g; K1, .04g; $CoSO_4.7H_2O$, .001g; Na_2SeO_3, .002g.

[5] -provided per kg diet: thiamine·HC1, 4 mg; Riboflavin, 8 mg; Niacin, 60 mg; D-Ca-pantothenate, 22 mg; pyridoxine·HC1, 7 mg; biotin, .33 mg; Vitamin B_{12}, .020 mg; folic acid, 1 mg; Vitamin A, 400 IU, Vitamin D_3, 600 ICU; Vitamin E, 22.5 IU.

constituents were provided according to NRC (1984) recommendations. To minimize feed wastage by the chickens, feeders were maintained only two-thirds full. Some feed was observed in the litter trays, although it was minimal and appeared consistent among experimental groups. Weekly feed consumption was estimated from weekly differences in feed plus feeder weights. Body weight gain, feed consumption and mortality were measured in each experiment.

Experiment 1

Dietary treatments shown in Table 1 were employed to evaluate the effect of photoperiod, energy level and their interaction on rate of gain, feed consumption, feed efficiency and on the 24 hour (circadian) rhythm of metabolic and blood parameters. Two light treatments (16L:8D and constant light) were employed. The sampling times were 0300h and 1500h, thus resulting in a 2 x 2 x 2 factorial arrangement of treatments (i.e., 2 photoperiods x 2 diets x 2 sampling times). The experimental design was completely randomized. Experimental diets were fed from day 1 to day 28 posthatching to triplicate groups of 6 male chicks each per treatment.

For energy retention, at the beginning of each experiment, 6 chicks of each group with body weights near the mean of the experimental birds were selected for initial carcass analysis. Upon terminating the experiment, birds were weighed and killed by cervical dislocation. The feathered carcass of each

chicken was then ground through a Hobart meat grinder. The ground carcasses were pooled for each replicate within the various experimental groups, thoroughly mixed and a ca 500g sample was taken. The representative sample was then dried for 72h in a forced-air drying oven set at 60°C. The dried material was finely ground in a Wiley mill for analysis. Each sample was analyzed in duplicate for total gross energy of carcass and expressed as a fraction of the metabolizable energy consumed to obtain percent energy retention.

Upon terminating the experiment, blood samples were collected from chicks by cardiac venipuncture using a heparinized needle and syringe. For free fatty acid determination, blood samples of 18h fasted birds were collected in non-heparinized containers and sodium citrate was used as the anticoagulant.

Red blood cells were removed by centrifugation at 200x g for 5 minutes and the plasma samples were cooled in ice before storage. Samples were stored at - 20C until needed. Plasma Triiodothyronine (T_3) and thyroxine (T_4) were determined using kits and procedures provided by Dade Baxter Travenol Diagnostics, Inc. (Cambridge, MA). Plasma free fatty acid concentration was determined using the kit and procedure supplied by Wako Pure Chemical Industries (Osaka, Japan). Plasma glucose and triglycerides were determined using kits and procedures provided by Sigma Chemical Company (St. Louis, MO).

In vivo hepatic lipogenesis was determined according to the method of Saadoun and Leclercq (1987) with little modification. Six birds per diets and per light treatment were starved for 14h and refed for 4h, and six fully fed birds per diet and per light treatment were injected intraperitoneally (IP) with 1.54 mCi tritiated water in 1 ml saline solution. Exactly 10 min post injection, the birds were killed by cervical dislocation and the livers were quickly removed, accurately weighed, and frozen on dry ice.

The frozen liver samples were ground into powdered form. About 1g of each liver sample was lyophilized, added to 50 ml diethyl ether, and extracted in a soxhlet apparatus. Lipids were weighed after evaporation of the solvent. Forty milliliters KOH in ethanol was added to each beaker and saponified for 10 minutes at 40°C. Unsaponified material was extracted with 50 ml hexane. The remaining soap solution was acidified by the addition of 10 ml 6N HCl. Fatty acids were quantitatively collected by washing four times with 50 ml hexane each time. One ml of hexane-fatty acids was placed in a scintillation vial and 10 ml of counting solution (Biofluor) added. Counting was done in a beta counter for 1 min. Rate of in vivo liver lipogenesis was determined as dpm/g liver/10 min.

After collection of blood from 18h fasted birds for plasma free fatty acids (FFA) analysis, the birds were euthanized and the abdominal fat-pads were removed immediately and placed in saline at room temperature for the in vitro lipolysis determination.

About 500 to 600 mg adipose tissue slices were prepared using a hand microtome and placed in flask plus medium according to the method of Calabotta et al. (1985). The flask was gassed with O_2:CO_2 (95:5) for 30 sec., stoppered with a teflon bung, and incubated at 37°C for 2h in a shaking water bath. Tissue was removed from each flask after 2 h and rinsed with saline into the flask. FFA concentration of medium was determined using WACO kits. This WACO test kit is an in vitro enzymatic colorimetric method for the quantitation of non-esterified (or free) fatty acid in serum. Lipolysis was expressed as microequivalents of FFA mobilized into the media per 2h per 100 mg tissue.

Dependant variables measured were body weight gain, feed consumption, feed efficiency (gain/feed), plasma concentrations of T_3, T_4, FFA, blood glucose, rate of in vivo liver lipogenesis, energy retention and rate of in vitro adipose tissue lipolysis.

Data were analyzed by analysis of variance and significance of photoperiod, diets, sampling time and their interactions were tested.

Experiment 2

This experiment was conducted to determine the effects of sex, photoperiod, and energy restriction and their interaction on growth, feed intake and feed efficiency of broiler chickens. The treatment design was a 3 x 2 x 2

factorial; the experimental design was completely randomized. The composition of the basal diets is presented in Table 1.

A total of 108 male and 108 female broiler chicks were utilized in this study. A total of 54 males and 54 female chicks one day posthatching, were randomly assigned to 18 groups in each of two rooms. Three experimental groups were then randomly allotted to each of the experimental diets under a 16 h light: 8h dark (16L:8D) photoperiod or constant light (CL). The three experimental diet treatments were: 1) the high energy diet fed ad libitum; 2) the low energy diet fed ad libitum; and 3) the high energy diet restricted to a daily caloric intake equal to that of treatment 2.

Groups receiving restricted quantities of feed were fed in two installments: at 0800 and 1700 hr. The amount received was based on the previous day's consumption by their respective ad libitum groups fed the low energy diet. To accomplish this, experimental groups fed ad libitum started and finished the experiment 1 day prior to the other experimental groups.

Data collected included weekly feed intake, weight gain, feed consumed, and feed efficiency during light and dark hours.

Data were statistically analyzed by analysis of variance using the GLM procedure of SAS (1982). The significance of the main effects of photoperiod, diets and sex, and each of the 2 - and the 3 - way interactions were measured for each dependent variable.

Results

Experiment 1

Both dietary energy concentration and light treatment significantly ($P<.01$) affected gain, feed intake and gain/feed ratio (Table 2). Birds grown under 16L:8D and fed the high energy diet achieved significantly higher body weights at 4 weeks of age. Birds fed the low energy diet achieved higher body weight when housed under constant light. This light treatment x dietary energy concentration interaction was also found to be significant ($P<.0001$) for feed consumption and gain/feed ratio.

Light treatment, sampling time and diet significantly ($P<.05$) affected the metabolic parameters measured (Table 3). Plasma triglyceride concentrations were higher in both birds housed under a 16L:8D photoperiod and instant light at the PM sampling time, but light treatment effects were not noticeable at the PM sampling time. Birds fed the low energy diet and housed under constant light exhibited the lowest concentration of plasma triglyceride. Plasma T_3 concentrations were higher in birds housed under 16L:8D, and sampling time differences were only observed in birds fed the high energy diet. Plasma T_4 concentrations were markedly higher in birds fed the low energy diet, and little affected by sampling time. Plasma glucose concentrations were significantly ($P<.01$) higher in birds fed high energy diet and housed under a 16L:8D photoperiod. Plasma glucose concentrations were slightly higher during the PM sampling time. Diets x light treatment interaction significantly ($P<.05$) affected

TABLE 2

Effect of diets, age and light treatment on body weight gain, feed consumption and feed efficiency[1]

Age, Wks	Diet[6]	Gain[2,5] 16L:8D	Gain[2,5] CL	Feed Consumed[2,4,5] 16L:8D	Feed Consumed[2,4,5] CL	Gain/feed[2,5] 16L:8D	Gain/feed[2,5] CL
		g		g		g/kg	
0	HE	88	100	94	104	936	962
	LE	67	83	94	105	713	791
2	HE	290	307	396	387	751	793
	LE	235	253	413	431	569	587
3	HE	605	589	847	822	714	717
	LE	502	519	875	874	574	595
4	HE	913	889	1406	1334	650	666
	LE	743	767	1462	1439	508	533
	pSE[7]		28.5		76.1		67.4

[1]Data are means of 3 groups of 6 male chicks each per treatment, fed the experimental diets from day 1 to day 28 posthatching.

[2]The main effect of light treatment was significant ($P<.01$).

[3]The main effect of diets was significant ($P<.0005$).

[4]The main effect of age was significant ($P<.0001$).

[5]The diets x light treatment interaction was significant ($P<.0001$).

[6]HE = high energy diet fed ad libitum; LE = low energy diet fed ad libitum.

[7]pSE - pooled standard error.

TABLE 3

Effect of light treatments, diets and sampling time on thyroxine (T_4), triiodothyronine (T_3), plasma free fatty acid (PFFA), glucose, triglyceride (TG), lipogenesis, lipolysis and energy retention in broiler chickens at 4 weeks of age[1]

Variable	Sampling Time[3]	Diets[2] HE 16L:8D	HE CL	LE 16L:8D	LE CL	pSE[4]
TG, mg/dl[5-7]	AM	267	197	269	174	47.3
	PM	367	361	349	304	
T_3, ng/dl[5-8,11]	AM	2.44	2.36	2.52	2.42	.276
	PM	2.93	2.57	2.57	2.46	
T_4, μg/dl[8,9,11]	AM	28.5	20.5	37.4	36.0	.85
	PM	24.1	20.2	35.2	31.8	
PFFA,μEq/L[5-9]						
	AM	200	346	326	330	88.1
	PM	244	354	288	315	
Glucose, mg/100 ml[8,9]	AM	358	308	352	313	78.5
	PM	379	356	363	321	
Lipolysis, PM μEq/2 h·mg tissue[5,8]		.50	.65	.47	.50	.121
Lipogenesis, dpm x 10^3/g liver·10 min (Starved-Refed)[5,8]	PM	4.5	3.0	3.6	2.8	1.63
Energy retention, %[5,8]	PM	63.1	55.2	52.8	51.8	2.77

[1]Data are means of 6 male chicks each.
[2]HE = high energy diet fed ad libitum.
LE = low energy diet fed ad libitum.
[3]Sampling times were: 300 h (AM) and 1500 h (PM).
[4]pSE = pooled standard error.
[5]The main effect of light treatment was significant (P<.05)>.
[6]The main effect of sampling time was significant (P<.05).
[7]The light treatment x sampling time interaction was significant (P<.05).
[8]The main effect of diets was significant (P<.01).
[9]The diets x light treatment was significant (P<.05).
[10]The effect of diet x sampling time x light treatment was significant (P<.001).
[11]The effect of diets x sampling time was significant (P<.05).

plasma glucose concentration. Plasma FFA concentrations were higher in birds housed under constant light. Birds fed the low energy diet exhibited higher PFFA concentration under 16L:8D, but lower concentrations under constant light.

Lipolysis was higher in birds fed the high energy diet and in birds housed under constant light. Lipogenesis and energy retention were significantly higher in birds fed the high energy diet and in birds housed under a 16L:8D photoperiod.

Experiment 2

Light treatment significantly ($P<.01$) affected gain and feed consumption, but not gain/feed ratio (Table 4). The light effect was most pronounced in birds fed the high energy diet, and was not observed in birds fed restricted amounts of feed twice daily.

In birds fed the high energy diet ad libitum, the 16L:8D photoperiod increased cumulative gain by an average of 13% and feed consumption by 16%. Within light treatment, males gained more, consumed more feed, and had a higher feed efficiency than females. Both light treatment and diet energy concentration significantly ($P<.05$) affected the percent of daily feed consumed during the period 2300 h to 700 h (Table 5). The percent of feed consumed during this period declined with age; within age and light treatment, birds fed the low energy diet consumed more of their daily feed during these hours.

TABLE 4

Effect of light treatment, diets and sex on 49 days body weight gain, feed intake and feed efficiency of broilers[1]

Variable	Sex	Light treatment[3]	Diets[2] HE	LE	HER	pSE[8]
Cumulative Gain, g[4,6]	M	LD	2538	2057	2135	
	M	CL	2184	1903	2134	
	F	LD	2234	1957	2043	78.6
	F	CL	2042	1891	1971	
Cumulative feed intake, g[4,6]	M	LD	5205	5301	3745	
	M	CL	4378	5938	3724	
	F	LD	4686	5130	3729	186.4
	F	CL	4148	5064	3607	
Cumulative Gain/feed, g/kg[6,7]	M	LD	487	388	570	
	M	CL	499	332	573	
	F	LD	477	382	548	52.6
	F	CL	490	374	546	

[1]Data are means of triplicate group of 6 chicks each per treatment, fed the experimental diets from day 1 to day 49 posthatching.

[2]HE = high energy diet fed ad libitum; LE = low energy diet fed ad libitum; HER = high energy diet restricted to caloric intake of LE birds; provided in two meals per day.

[3]LD = 16 light:8 dark; CL = constant light.

[4]The main effect of light was significant ($P<.01$).

[5]The main effect of sex was significant ($P<.05$).

[6]HE versus LE and HER was significant ($P<.01$).

[7]LE versus HER was significant ($P<.001$).

[8]Pooled standard error.

TABLE 5

Percent of daily feed consumed during the period 2300h to 0700h[1,2]

	Light treatment[3,4]			
	16L:8D		CL	
	Diet[5,6]			
AGE,WKS	HE	LE	HE	LE
1	.26	.04	11.64	10.12
2	.60	.56	12.08	10.91
3	.24	.19	12.11	10.39
4	.23	.18	12.03	10.43
5	.15	.13	8.46	6.47
6	.17	.15	7.71	7.23
7	.15	.16	8.49	6.55
pSE[7]	.114		1.432	

[1]The period 2300h to 700h coincided with the scotophase of birds housed under 16L:8D: photoperiod.

[2]Data are means of six replicate groups of 6 chicks each; i.e. 3 replicate groups of male chicks and 3 replicate groups of female chicks.

[3]LD = 16 light:8 dark; CL = constant light

[4]The main effect of light was significant ($P<.05$).

[5]The main effect of diet was significant ($P<.05$).

[6]He = high energy diet fed ad libitum; LE = low energy diet fed ad libitum.

[7]Pooled Standard error

Discussion

Growth in chickens and other species is a complex process which is controlled by a multiplicity of hormones. The final expression of growth is the result of interactions between nutritional, environmental and genetic factors with the endocrine secretions. Obviously, these interactions can be manipulated by management practices to maximize growth rate and feed efficiency and to optimize carcass characteristics.

There has been great interest in developing a means of increasing both the yield and quality of poultry meat. Techniques include early nutrient restriction to reduce the size of the abdominal fat pad and carcass fat at slaughter (Pokniak and Cornejo, 1983; Plavnik et al., 1986; Arafa et al., 1983), exogenous thyroid hormone treatment to alter fat deposition (May, 1980), and regulating the photoperiod to induce changes in growth rate and fat deposition (Cave, 1980; Robbins et al., 1984; Osei, 1987).

A multitude of hormones appear to be required for growth. In both birds and mammals, there is a requirement for growth hormone (GH), thyroxine (T_4), triiodothyronine (T_3) and probably for insulin, somatomedins, and other circulating growth factors, namely prolactin and androgens.

Environmental factors play a major role on the actions of hormones that respond to the body activities. Among these environmental factors are light, temperature, rainfall, humidity, parasites and predators to name a few. The

endocrine systems and the nervous system are modulators of the body metabolic functions. The role of the endocrine system is to keep in proper measure or proportion the activity of different organs. Environmental factors act directly on the central nervous system (CNS) which in turn will send signals to necessary organ(s) and actions to the target tissue. For instance, exposure to cold has been reported to be associated with an increase in several aspects of thyroid function in the domestic fowl (Kuhn et al., 1982). Buckland et al. (1976) reported up to a four fold increase in plasma corticoid levels in birds subjected to continuous light compared to birds under different intermittent light regimes. Osei (1981) reported higher corticosterone levels in birds subjected to constant light as compared with 16L:8D reared birds. This might indicate a trend in which stress due to constant light might overstimulate the adrenal gland directly or indirectly to produce higher plasma hormone levels. Stress situations induce a hyperactivity of adrenal glands under a preceding stimulation by hypothalamic CRH and pituitary ACTH.

Nutritional factors do have significant effects on body composition in broilers. The rate of protein deposition in muscle will reflect both the ability of the diet to provide substrate for growth, as well as its ability to evoke a regulatory response which activates the anabolic processes involved in growth. These factors will depend not only on the quality of the diet,but also on the quantity of food consumed. For instance, growth suppression is to be expected with very low protein diets or with food restriction. In general, high energy

diets have advantages if body weight gain and food efficiency are considered. If carcass quality is taken into account, the benefits of high energy diets are less (Freeman, 1983). These circulating nutrients and metabolites work either directly on CNS, hypothalamic or insulin and on circulating growth factors in the body. Genetic potential act directly on tissue growth and indirectly through CNS, hypothalamic, pituitary gland, gonad and thyroids.

In experiment 1, it was found that a 16L:8D photoperiod enhanced growth of birds fed a high energy diet but depressed growth of birds fed a low energy and housed under CL. This may have been due to more lighted hours and hence altered feeding activity. This was tested more completely in experiment 2. In this experiment, birds housed under 16L:8D achieved a higher body weight at 49d of age when fed either the high or low energy diet. Furthermore, birds housed under constant light consumed only 10% of their daily feed allowance during the period 2300h to 700h. The amount of feed consumed during these "dark" hours was not substantially affected by diet energy concentration. It thus appears that growth rate differences between light treatments were not simply the result of changes in feeding.

That changes in feeding behavior were not the sole factor responsible for enhanced growth of chickens housed under 16L:8D is substantiated by the metabolic data (Table 3). At 4 wk of age birds housed under 16L:8D had higher concentrations of circulating TG, T_3, T_4 and glucose thus indicating that they were in a more positive anabolic state. Birds housed under CL exhibited

an increased rate of lipolysis, a corresponding increased concentration of PFFA, and a reduced rate of lipogenesis. The sum affect of these differences was an increased rate of energy retention in 16L:8D birds, which was most pronounced when the high energy diet was fed.

In these studies, a period of growth depression (decreased growth velocity) occurred in both male and female broiler chickens under CL approximately 3 weeks after beginning a constant light period. Since depressed growth occurred in both males and females, it was decided to use male chicks for the rest of the experiments. The results of the growth trials were similar to those reported by Deaton et al., 1978; Robbins et al., 1984 and Osei, 1987. The interaction between lighting programs, dietary energy and feeding regimes from these studies show that body weight gain was significantly affected by the lighting programs and feeding regimes. The birds under constant light program were significantly smaller in body size than those under 16L:8D program. Apart from depression from light effect, the retarded growth rate of birds under constant light might be due to their constant movement, so that they may have utilized more energy for exercise and less toward weight gain. The birds subjected to low energy diet ad libitum feeding consumed significantly more feed than those subjected to high energy ad libitum feeding regime, regardless of lighting program as indicated in Table 4. This shows that birds fed low energy diet ad libitum consumed more feed to meet their energy requirement. This reflected a poorer feed efficiency rate which indicates over consumption of

feed in this group of birds. In broilers, the capacity of the gastro-intestinal track is reported to be the limiting factor for ad libitum feed intake, while in layer-type birds regulation by hypothalamic hormones is more important (McCarthy and Siegel, 1983; Fisher, 1984).

Beane et al., (1977) found that restricting broiler intake to 85% of full-fed broiler reduced growth rate. Holder et al., (1977) removed access to feed for 2 h two times each day (4h/day) but found no effect on either growth rate or feed conversion. Conard and Kneuzel (1978), using a dietary energy level of 3460 kcal ME/kg and 16h light: 8h dark (16L:8D), found that five 1 1/2 or 2h meal/day, significantly increased body weight. Feed conversion changed from 2.16 to 1.96 but this change was not statistically significant. These researchers postulated that domestic fowls are "nibblers", eating throughout the day, and that forcing broiler chickens to become periodic feeders might improve their performance.

Yule et al. (1979) reported that results with restricted feeding may depend on environmental temperature. Using 23h of light/day and restricting access to feed for 8h each day, they found that during cold weather (outside temperatures 8.9°C, inside not specified) feed conversion was significantly improved from 2.15 to 2.11 with no effect on growth rate. In "summer" (outside temperature 22.9°C, inside not specified) there was no significant effect on either body weight or feed conversion.

Under the light program used in these studies, the growth performance of the birds subjected to constant light was clearly inferior to that of the birds subjected to 16L:8D. These findings are in agreement with reports of Cherry et al. (1980) who observed that broilers subjected to an intermittent photoperiod regime had significantly greater weight gain than broilers reared under constant light. The higher body weight gains and feed consumption for birds fed the high energy diet ad libitum, and better feed efficiency in the HER regime reported in our studies are in agreement with the findings of Beane et al. (1979) and Diab et al., (1987). They stated that during 14-42 days, greater gains and feed consumption with lesser feed efficiency were noted for the full fed groups of chickens than for the restricted groups.

The high dietary energy level of 3300 Kcal ME/kg used in our studies resulted in significantly higher body weight gain and better feed efficiency value than the low dietary metabolizable energy level of 2475 Kcal ME/kg; although feed consumption levels were lower for the high metabolizable energy level groups. Since constant light depressed the body weight in all our studies, these studies indicate that combining a photoperiod of 16L:8D with restricted feeding of high dietary energy will result in a substantial and significant improvement in overall performance of broilers.

In all these studies, male chickens performed better than females There is evidence that androgens exert a positive effect on growth in the early stage, and this would explain the more rapid growth in male fowl as observed in our

studies. Moreover, there is also a marked tendency for male chickens to have higher circulating concentration of growth hormone (GH) than females (Harvey et al., 1979b).

Photoperiod can entrain feeding patterns which can be manipulated by feeding schedules. Halberg and his associates (as reported by Romsos and Leveille (1977)) have demonstrated that allowing human beings to eat a 2000 kcal meal in the morning resulted in a greater weight loss than when the 2000 kcal meal was consumed in the evening. Eating followed by reduced activity appears to be important for optimizing feed efficiency.

In addition, meal feeding administered on a fixed daily schedule entrains peaks of activity of intestinal enzymes (Stevenson and Fierstein, 1976). Therefore, timing each meal relative to periods of physical activity and endogenous rhythms of metabolic enzymes and metabolites may be important for improved conversion of feed to animal protein.

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PART III

EFFECTS OF LIGHT TREATMENT AND DIET AND THEIR INTERACTION ON GROWTH AND ENERGY METABOLISM OF BROILER CHICKENS.

Abstract

Four experiments were conducted, using growing male broiler chicks to examine the effects of light treatment (16L:8D versus constant light) on growth and a variety of metabolic parameters. The diet used contained 23% CP and 3300 kcal ME/kg diet. The results indicated that birds reared under 16L:8D performed better than birds reared under constant light. Depression in body weight of birds housed under constant light was not pronounced until after three weeks of age. Constant light significantly depressed hepatic lipogenesis and energy retention. Circulating concentrations of triglyceride, glucose, triiodothyronine (T_3)and thyroxine (T_4) were depressed in birds housed under constant light compared to birds reared under 16L:8D. These changes are in accordance with the well-known inhibitory effect of stress on thyroid and other endocrine functions in birds and mammals. Constant light increased plasma free fatty acid concentration and rate of lipolysis. Tibia weight, length and epiphyseal plate thickness were uniformly and slightly reduced in birds reared under constant light.

Introduction

Effects of photoperiod have been observed on growth and metabolic parameters by many researchers with different results. Osei (1987) reported that broilers grown under constant light versus a 16L:8D photoperiod had

reduced rate of growth, reduced efficiency of energy retention, reduced rates of liver lipogenesis and reduced jujunal glucose uptake, in addition to reduced concentrations of plasma T_3 and T_4. Deaton et al., (1978) observed a significantly better feed conversion in commercial broilers reared under an intermittent-lighting regime than broilers reared under a continuous lighting regime.

Skeletal growth involves the formation of cartilage that is subsequently replaced by bone. This is particularly evident during growth in length of long bones in which linear growth continues as long as cartilage formation in the epiphyseal growth plate exceeds its replacement by bone. In mammals, thyroid hormones have been shown to influence cartilage formation and the ossification and histology of long bones during their growth and maturation (Schwartz, 1983). However, there is little information available concerning the role of the photoperiod and thyroid hormones on skeletal growth of poultry, other than its influence on bone length (Burch et al., 1982). Under conditions of stress the plasma corticoid levels of chickens can increase up to fourfold (Buckland et al., 1976). Increased corticosterone levels due to abnormal lighting conditions have been reported by Meier and Fivizzan (1975) and Osei (1981).

Some commercial broilers are now being reared under photoperiodic housing systems (Weaver, 1977) with different photoperiods and intermittent light under moderate temperature conditions. Results of these and other studies

indicate that the presence of a photoperiod is necessary for normal growth and development of broiler chicks.

The effect of constant light versus a photoperiod on nutrient metabolism and growth are not well understood. Additional information is needed, particularly given the fact that many laboratory nutrition studies with poultry are conducted under conditions of constant light and a better understanding of the effect of constant light versus a photoperiod on nutrient metabolism and growth is needed because of the sharp increase in feed and fuel costs..

The objectives of this study were to determine the effects of light treatment on growth and on the 24 hour (Circadian) rhythm of energy retention, rate of liver lipogenesis, rate of lipolysis using abdominal fat pad explants, plasma concentrations of T_3, T_4, free fatty acids, triglycerides, blood glucose, tibia weight, length and epiphyseal plate thickness.

Materials and Methods

Shaver Color-Pac sexed broiler chicks were used in experiment 1; while Indian River crossbred feather-sexed chicks were used in experiments 2-4. Fertile eggs were obtained from breeder flocks maintained at the University of Tennessee and hatched in the University hatchery. One day posthatching chicks were sexed and all morbid, unthrifty chicks were discarded. The remaining chicks were individually wingbanded and randomly distributed to treatment groups.

Chickens were housed in electrically heated battery brooders kept in light proof, heated, and ventilated rooms. In one room, lights remained on 24 hours per day. In the other room a 16 hour light:8 hours dark photoperiod was imposed. Light intensity at bird level measured 14.5 lux. The temperature of both rooms, monitored twice daily, did not on any day differ between rooms by more than 1°C, and averaged 28°C through the experimental periods. The chickens were housed in electrically-heated battery-brooders through 4 weeks of age, then transferred to unheated grower batteries for the remaining experimental period. All chicks were started in the appropriate light treatment at 1 or 5 days posthatching. Each experiment lasted 4 to 7 weeks.

Feed and water were provided ad libitum. A soybean meal based semi-purified diet was used (Table 1). The experimental diet contained 23% CP and 3300 kcal ME/kg. All other constituents were provided according to NRC (1984) recommendations. To minimize feed wastage by the chickens, feeders were maintained only two-thirds full. Some feed was observed in the litter trays, although it was minimal and appeared consistent among experimental groups. Weekly feed consumption was estimated from weekly differences in feed plus feeder weights. Body weight gain, feed consumption and mortality were measured in each experiment.

TABLE 1

Composition of the experimental diet[1]

Basal Diet	%
Dextrose	15.00
Soybean Meal(47.47% CP[2])	48.35
Corn starch	9.75
Soy oil	13.87
Salt premix[3]	5.37
Vitamin premix[4]	0.20
Choline chloride	0.40
DL - methionine	0.23
Cellulose	.83
	100.00

[1] -Diet was formulated to contain 23% CP; 3300 kcal ME/kg.

[2] -As analyzed.

[3] -Provided per kg diet: $CaCO_3(PO_4)_2$, 28g; K_2HPO_4 9g; NaCl, 8.8g; $MgSO_4.7H_2O$, 3.5g; $MnSO_4.H_2O$, .65g; Ferric citrate, 5g; $ZnCO_3$, .1g; $CuSO_4.5H_2O$, 0.02g; $Na_2MoO_4.2H_2O$, .001g; K1, .04g; $CoSO_4.7H_2O$, .001g; Na_2SeO_3, .002g.

[4] -Provided per kg diet: thiamine·HCl, 4 mg; Riboflavin, 8 mg; Niacin, 60 mg; D-Ca-pantothenate, 22 mg; pyridoxine·HCl, 7 mg; biotin, .33 mg; Vitamin B_{12}, .020 mg; folic acid, 1 mg; vitamin A, 400 IU, Vitamin D_3, 600 ICU; Vitamin E, 22.5 IU.

Experiment 1

This experiment was conducted to determine the effects of photoperiod, sampling time(3 AM and 3PM), and their interaction, if any, on the 24 hour (circadian) rhythm of several metabolic and blood parameters. All birds were fed the diet (Table 1) ad-libitum under two photoperiods 16L:8D and constant light. The experimental design was completely randomized. The experimental diet was fed from day 1 to day 28 posthatching to triplicate groups of 6 male chicks each per treatment.

For energy retention, at the beginning of each experiment, 6 chicks of each group with body weights near the mean of the experimental birds were selected for initial carcass analysis. Upon terminating the experiment, birds were weighed and killed by cervical dislocation. The feathered carcass of each chicken was then ground through a Hobart meat grinder. The ground carcasses were pooled for each replicate within the various experimental groups, thoroughly mixed and a ca. 500g sample was taken. The representative sample was then dried for 72h in a forced air drying oven set at 60°C. The dried material was finely ground in a Wiley mill for analysis. Each sample was analyzed in duplicate for total gross energy of the carcass and expressed as fraction of the metabolizable energy consumed to obtain percent energy retention.

Upon terminating the experiment, blood samples were collected from chicks using a heparinized needle and syringe by cardiac venipuncture into NH_4-heparinized sample tubes (Sarstedt). For free fatty acid determination, blood samples of 18h fasted birds were collected in non-heparinized containers and sodium citrate was used as the anticoagulant, since heparin is known to stimulate the activity of lipoprotein lipase which acts upon triglycerides associated with blood lipoproteins to release free fatty acids.

Red blood cells were removed by centrifugation at 200x g for 5 minutes and the plasma samples were cooled in ice before storage. Samples were stored at -20°C until needed. Plasma T_3 and T_4 were determined using kits and procedures provided by Dade Baxter Travenol Diagnostics, Inc. Plasma free fatty acids were determined using the kit and procedure supplied by Wako Pure Chemical Industries. Plasma glucose and triglycerides were determined using kits and procedures provided by Sigma Chemical Company.

In vivo hepatic lipogenesis was determined according to the method of Saadoun and Leclercq (1987) with little modification. Six birds per diet and per light treatment were starved for 14h and refed for 4h, and another 6 fully fed birds per diet and per light treatment were injected intraperitoneally (IP) with 1.54 mCi tritiated water in 1 ml saline solution. Exactly 10 minutes post injection, the birds were killed by cervical dislocation and the livers were quickly removed and accurately weighed.

The liver samples were frozen and ground into powdered form. About 1g each of the liver samples were extracted in 50 ml diethyl ether in a Soxhlet apparatus; lipids were weighed after evaporation of the solvent. Forty ml KOH in ethanol was added to each beaker and saponified for 10 minutes at 40°C. Unsaponified material was extracted with 50 ml hexane. The remaining soap solution was acidified by the addition of 10 ml 6N HCl. Fatty acids were quantitatively collected by washing 4 times with 50 ml hexane each time.

One ml of hexane-fatty acids were placed in a scintillation vial and 10 ml of counting solution (Biofluor) added. Counting was done in a beta counter for 1 minute. Rate of in vivo liver lipogenesis was determined as dpm/g liver/10 min.

After collection of blood from 18h fasted birds for plasma free fatty acids (FFA) analysis, they were killed and abdominal fat-pad tissues were removed immediately and placed in saline at room temperature for the in vitro lipolysis determination.

About 500 to 600 mg adipose tissue slices were prepared using a hand microtome and placed in flask plus medium according to the method of Calabotta et al. (1985). The flask was gassed with O_2:CO_2 (95:5) for 30 sec., stoppered with a teflon bung, and incubated at 37°C for 2h in a shaking water bath. Tissue was removed from each flask after 2h and rinsed with saline into the flask. FFA concentration of medium was determined using (WACO) kits. This WACO test kit is an in vitro enzymatic colorimetric method for the

quantitation of non-esterified (or free) fatty acid in serum. Lipolysis was expressed as microequivalents of FFA mobilized into the media per 2h per 100 mg tissue.

Dependent variables measured were body weight gain, feed consumption, feed efficiency, plasma concentrations of T_3, T_4, FFA, TG, blood glucose, rate of in vivo liver lipogenesis, energy retention and rate of in vitro adipose tissue lipolysis.

Data were analyzed by analysis of variance and significance of photoperiod, diets, sampling time and their interactions were tested. Dependent variable measured at 2 and 4 weeks of age were plasma concentration of T_3, T_4, FFA, TG, rate of liver lipogenesis, energy retention and rate of lipolysis using abdominal fat pad explants.

Experiment 2

This was conducted to determine the effect of photoperiod on broiler growth, T_3,T_4, and tibia weight, length and epiphyseal cartilage plate thickness.

Nine replicate groups of 6 male chicks each were housed under each of 2 light treatments: 16L:8D and constant light. Chicks which died during the first 4 days were replaced with chicks of the same body weight. Body weights were measured every 3 or 4 days through 49 days of age. Feed intake and gain:feed were regularly measured beginning on day 5 posthatching.

At 1, 2, 3, 4, 5, 6, and 7 weeks of age, one randomly selected replicate group of chicks per light treatment was used to collect blood and bone data. Chicks were bled via heart puncture; plasma was harvested as in experiment 1 and analyzed for T_3 and T_4. The chickens were killed and both tibias were removed. The tibias were weighed and the length of the bone was measured. The width of the epiphyseal cartilage plate was measured according to the method and procedure of Herbert et al., (1943).

The tibias were split at the proximal end in a sagittal plane, and fixed in neutralized 10% formalin. Prior to staining, the bone halves were washed thoroughly in running water and immersed in acetone for at least 1 h and washed again. They were then immersed for about 1-1/2 minutes in 2% silver nitrate solution and exposed to a strong light, while kept under water, until calcified parts appeared dark brown. They were then fixed in a 10% solution of sodium thiosulfate for about one-half of a minute, followed by thorough washing under running water.

The width of the uncalcified proximal epiphyseal cartilage was measured under the low power of a microscope using a micrometer eye piece which is calibrated with stage micrometers. A minimum of 8 to 10 readings were made across the section and the average was calculated. The result was expressed in micrometers.

Dependent variables for experiment 2 were body weight gain, feed consumption, feed efficiency, plasma T_3 and T_4, and tibia weight, length and

epiphyseal cartilage plate thickness. Data were statistically analyzed by analysis of variance using the GLM procedure of SAS (1982). The significance of the main effects of photoperiod and age as well as their interaction were tested.

Experiment 3

This was conducted to determine the effects of photoperiods and age on the rate of gain, feed consumption, feed efficiency, Plasma T_3 and T_4, energy retention capabilities and rate of liver lipogenesis.

Twenty replicate groups of 6 male chicks each were housed under each of 2 light treatments: 16L:8D and constant light. Chicks which died during the first 4 days were replaced with chicks of the same body weight and under the same light treatment. Body weights were measured every week through 49 days of age. Feed intake and feed efficiency were regularly measured beginning on day 1 post-hatching.

On the 3rd week, 3 replicates of 6 chicks each per light treatment were bled via heart puncture as described in experiment 1 to collect blood; then killed for energy retention. Moreover, another 3 replicates of 6 chicks each per light treatment were used for lipogenesis as described in experiment 1.

From the remaining 16 replicates per light treatment, 8 replicates each were interchanged into alternate light treatments. At seven weeks of age, the same procedures used at 3 weeks of age were repeated to collect the samples.

Dependent variables for experiment 3 were body weight gain, feed consumption, feed efficiency, plasma T_3 and T_4, energy retention and rate of liver lipogenesis.

Data were statistically analyzed by analysis of variance using GLM procedures of SAS (1982). The significance of the main effects of photoperiod and age as well as their interaction were tested.

Experiment 4

This experiment was conducted as a follow-up of experiments 1 - 3 to determine the effect of photoperiod, and age on the rate of gain, feed consumption, feed efficiency, Plasma T_3 and T_4, energy retention and rate of liver lipogenesis.

Twelve replicate group of 6 male chicks each were housed under each of 2 light treatments: 16L:8D and constant light (CL). Chicks which died during the first 4 days were replaced with chicks of the same body weight. Body weights were measured every week through 42 days of age. Feed intake and feed efficiency were regularly measured beginning on day 1 posthatching.

Blood samples were collected via heart puncture at the second week of age from two replicates (one replicate starved-refed and one replicate ad libitum fed) of chicks per each light treatment ; plasma was harvested and analyzed for T_3 and T_4; then killed for energy retention. Furthermore, another 2 reps as described above were used for lipogenesis as described in experiment 1.

The same procedures as described above were carried out at 4th and 6th weeks of age with the same number of chicks.

Dependent variables for this experiment were body weight gain, feed consumption, feed efficiency, plasma T_3 and T_4, energy retention and rate of liver lipogenesis. Data were statistically analyzed by analysis of variance using GLM procedure of SAS (1982). The significance of the main effects of photoperiod and age as well as their interaction were tested.

Results

Experiment 1

Light treatment significantly ($P<.0001$) affected gain, feed intake and gain/feed ratio (Table 2). Birds reared under a 16L:8D photoperiod achieved higher body weights and consumed more feed at 4 weeks of age than birds reared under constant light. The age x light treatment interaction was found to be significant ($P<.0001$) for both feed intake and gain/feed ratio.

Light treatment and sampling time significantly ($P<.05$) affected the metabolic parameters measured (Table 3). Plasma triglyceride concentrations were significantly ($P<.05$) higher in birds reared under a 16L:8D photoperiod at the PM sampling time. Triglyceride concentrations were slightly decreased with age under each light treatment.

Plasma T_3 concentrations were significantly ($P<.05$) higher in birds reared under 16L:8D and at the PM sampling time of each light treatment. The

TABLE 2

Effect of light treatment and age on body weight gain, feed consumed and feed efficiency[1-3]

Age, wks	Gain		Feed consumed		Feed efficiency	
	16L:8D	CL	16L:8D	CL	16L:8D	CL
	-------g-------		------g------		------g/kg----	
1	110	121	149	166	738	729
2	331	339	449	465	737	729
3	601	641	898	907	669	707
4	981	931	1502	1456	653	639
pSE[4]	26.8		24.8		117.7	

[1]Data are means of triplicate groups of 6 male chicks each per treatment, fed the experimental diet from day 1 to day 28 posthatching.

[2]For each variable, the effect of light treatment and age was significant ($P<.0001$).

[3]The age x light treatment interaction was significant ($P<.0001$).

[4]pSE - pooled standard error.

TABLE 3

Effect of light treatment and sampling time on measures of energy metabolism and plasma triglyceride (TG), plasma free fatty acid (PFFA), triiodothyronine and thyroxine concentrations in broilers[1]

		Light treatment[2]				
		16L:8D		CL		
Variable	Age,wks	AM[3]	PM[4]	AM[3]	PM[4]	pSE[5]
TG, mg/dl[6,7]						
	2	282	378	209	362	44.1
	4	262	308	219	263	66.1
T_3, ng/ml[6,7]						
	2	2.94	3.50	2.49	3.41	1.128
	4	2.06	3.49	1.59	2.09	1.016
T_4, μg/dl[6,7]						
	2	23.2	24.3	20.7	22.1	1.05
	4	44.1	30.0	38.9	26.1	1.14
Energy retention, %	2	---	53.0	---	50.8	3.19
	4	---	48.2	---	42.8	
PFFA, μEq/L						
	4	---	272	---	329	86.4
Lipolysis, μEq/2h·mg tissue	4	---	.22	---	.31	.115
Lipogenesis, dpm x 10^3/g liver·10 min (ad-libitum feeding)	4	---	3.9	---	2.9	.86

[1]Data are means of 6 male chicks each.

[2]The main effect of light treatment was significant ($P<.05$).

[3]AM - 0300 h; energy retention, PFFA, lipolysis and lipogenesis were not determined.

[4]PM - 1500 h.

[5]pSE = pooled standard error.

[6]The main effect of sampling time was significant ($P<.05$).

[7]The main effect of light treatment x sampling time was significant ($P<.05$).

main effect of light treatment x sampling time was significantly ($P<.05$) higher in birds housed under a 16L:8D at PM sampling time. Plasma T_4 concentrations were significantly ($P<.05$) higher in birds housed under 16L:8D, with little effect of sampling time at 2 weeks of age.

Plasma FFA concentrations were significantly ($P<.05$) higher in birds housed under constant light. Energy retention was significantly ($P<.05$) higher in birds reared under a 16L:8D photoperiod and this decreased with age. Constant light increased the rate of lipolysis. Lipogenesis was significantly ($P<.05$) higher in birds housed under a 16L:8D photoperiod.

Experiment 2

Birds housed under constant light showed greater body weight gain through week 3, while birds reared under a 16L:8D photoperiod surpassed them after the third week of age and this accelerated growth continued to show through week 7 (Table 4). Light treatment significantly ($P<.01$) affected feed intake. The light treatment x age interaction was found to be significant ($P<.05$) for gain, feed consumption, and gain/feed ratio.

Light treatment and age significantly ($P<.05$) affected the metabolic parameters measured (Table 5). Tibia weight, tibia length and epiphyseal plate

TABLE 4

Effects of photoperiod on body weight gain, feed consumed and feed efficiency[1-4]

Age, Wks	Gain(g)		Feed consumed (g)		Feed efficiency	
	16L:8D	CL	16L:8D	CL	16L:8D	CL
	g		g		g/kg.	
1	77	84	101	118	765	710
2	251	266	334	364	752	730
3	631	573	889	782	710	729
4	940	948	1408	1381	667	685
5	1402	1339	2220	2167	632	618
6	1810	1738	3140	3025	576	575
7	2118	2049	4117	3959	515	518
pSE[5]	33.1		50.5		45.1	

[1]Data are means of 3 groups of 6 male chicks each fed the experimental diet from day 1 to day 49 posthatching.

[2]For each variable except for feed consumed, the effect of photoperiod was not significant (P<.10).

[3]For each variable, the effect of age, "linear" was significant (P<.001).

[4]Age x photoperiod interaction was significant (P<.05)

[5]pSE = pooled standard error.

Table 5

Effect of light treatment on broiler growth, plasma T_3 and T_4 concentrations and skeletal development.

Age week	Light Treatment[3]	Variable[1,2] TW,g	TL,cm	EPT,μm[4,5]	T_3,ng/ml[4,5]	T_4,ng/dl[4]
1	16L:8D	.64	3.77	ND[6]	3.95	20.9
	CL	.66	3.78	ND[6]	2.74	17.3
2	16L:8D	3.01	5.62	1.15	2.93	29.7
	CL	3.30	5.60	1.16	2.19	25.8
3	16L:8D	3.88	6.35	1.24	2.93	27.3
	CL	3.67	6.34	1.15	2.89	25.7
4	16L:8D	10.10	8.59	1.26	2.47	34.2
	CL	9.96	8.37	1.17	2.36	32.8
5	16L:8D	15.32	9.88	1.43	1.55	36.8
	CL	14.02	9.52	1.20	1.15	30.6
6	16L:8D	18.02	10.75	1.30	1.47	42.4
	CL	19.41	10.95	.94	.95	36.7
7	16L:8D	23.47	11.66	1.47	1.68	52.8
	CL	21.39	11.64	1.01	.86	40.3
	pSE[7]	2.065	.429	.102	.505	6.06

[1]TW - Tibia weight; TL - Tibia length; EPT - Epiphyseal plate thickness; T_3 - triiodothyronine; T_4 - Thyroxine.

[2]Mean of 6 male chicks per treatment/age.

[3]16 Light:8 dark; constant light (CL).

[4]The age x light treatment interaction was significant ($P<.05$).

[5]The effect of light treatment was significant ($P<.0001$).

[6]ND - Not detected

[7]pSE - Pooled standard error.

thickness were uniformly and slightly higher in birds reared under a 16L:8D photoperiod. Light treatment significantly ($P<.0001$) affected epiphyseal plate thickness and plasma T_3 concentrations. Plasma T_3 concentrations decreased with age, while plasma T_4 concentrations increased with age. The age x light treatment interaction significantly ($P<.05$) affected epiphyseal plate thickness, plasma T_3 and T_4 concentrations.

Experiment 3

Birds housed under constant light grew faster than birds reared under 16L:8D up to the third week of age (Table 6), then birds underwent a depressed growth phase after the third week and this phenomena continued until the study was terminated at 7 weeks of age.

Birds housed under a 16L:8D photoperiod throughout had the highest body weight and feed consumption; while birds reared under constant light and subjected to 16L:8D after 3 weeks of age had the lowest body weight and feed consumption. Light treatment did not, however, affect gain/feed ratio.

Age and light treatment significantly ($P<.0001$) affected the metabolic parameters measured (Table 7). Plasma T_3 concentrations were highest in birds reared under 16L:8D and lowest in birds reared under constant light. Plasma T_3 concentrations decreased with age. Plasma T_4 concentrations were relatively the same under light treatments. Light treatment x age significantly ($P<.01$) affected the level of plasma T_4 concentrations. Lipogenesis was significantly

TABLE 6

Effects of photoperiods on broiler growth, feed intake and feed efficiency[1,2]

		Age (wks)						
Light	treatment[3]	1	2	3	4	5	6	7
Body wt, g	LD/LD	88[b]	266[c]	605[a,b]	1019[a]	1446[a]	1941[a]	2305[a]
	CL/CL	96[a]	296[a]	627[a,b]	970[a,b]	1376[a]	1805[b]	2167[b]
	LD/CL	89[b]	275[b,c]	597[b]	981[a,b]	1412[a]	1831[a,b]	2221[a,b]
	CL/LD	97[a]	291[a,b]	639[a]	944[b]	1427[a]	1818[b]	2140[b]
Feed intake, g	LD/LD	94[b]	333[a]	748[a]	1399[a]	2223[a]	3163[a]	4097[a]
	CL/CL	97[b]	351[a]	774[a]	1367[a]	2129[a]	3005[a]	3966[a]
	LD/CL	97[b]	341[a]	755[a]	1356[a]	2132[a]	3033[a]	4002[a]
	CL/LD	101[a]	347[a]	764[a]	1334[a]	2186[a]	3067[a]	3735[b]
Feed efficiency, g/kg	LD/LD	926[b]	797[b]	809[a,b]	729[a]	651[a]	614[a]	563[a]
	CL/CL	987[a]	843[a]	810[a,b]	709[a]	647[a]	601[a]	547[a]
	LD/CL	922[b]	806[b]	710[b]	724[a]	663[a]	604[a]	555[a]
	CL/LD	960[a,b]	840[a]	838[a]	708[a]	653[a]	593[a]	573[a]

[1]Data are means of 3 groups of male chicks each fed the experimental diet from day 1 to day 49 posthatching. Pooled standard errors were 65.7 for body weight; 105.1 for feed intake; and 29.1 for feed efficiency.

[2]Means within a column and under the same variable with no common superscripts are significantly different ($P<.05$) using LSD.

[3]LD/LD = 16L:8D photoperiod from hatching to day 49;
CL/CL = Constant light from hatching to day 49;
LD/CL = 16L:8D from hatching to 21 day; then constant light to day 49;
CL/LD = Constant light from hatching to 21 day; then 16L:8D to day 49.

TABLE 7

Effects of light treatment on T_3, T_4, Lipogenesis and energy retention in broiler chicks at 3 and 7 weeks of age[1]

Variable	Age, wks	Light Treatment[2,3] LD/LD	CL/CL	LD/CL	CL/LD	pSE[4]
Plasma T_3, ng/ml[5]	3	2.83	2.52	--	--	.380
	7	1.18	.75	.94	1.12	
Plasma T_4, μg/dl[6]	3	29.5	27.2	--	--	4.04
	7	27.1	25.3	23.0	28.5	
Lipogenesis, dpm x 10^3/g liver·10 min (starved-refed)=[5,6]	3	3.9	3.4	--	--	.32
	7	2.9	2.6	2.2	1.9	
Lipogenesis, dpm x 10^3/g liver·10 min (ad libitum feeding)[5,6]	3	3.8	3.2	--	--	
	7	2.7	2.5	1.6	1.6	
Energy retention, %[5,6]	3	47.6	42.1	--	--	1.06
	7	37.6	26.6	30.8	28.0	

[1]Data are means of 6 male chicks each.

[2]LD/LD = 16L:8D photoperiod from hatching to day 49.
CL/CL = Constant light from hatching to day 49.
LD/CL = 16L:8D from hatching to 21 day, then constant light to day 49.
CL/LD = Constant light from hatching to 21 day, then 16L:8D to day 49.

[3]The main effect of light treatment was significant ($P<.0001$).

[4]pSE = Pooled standard error.

[5]The main effect of age (wks) was significant ($P<.0001$).

[6]The main effect of light treatment x age was significant($P<.01$).

(P<.0001) high in birds housed under 16L:8D and low in birds first subjected to constant light and then 16L:8D. The rate of lipogenesis significantly (P<.0001) decreased with age. Light treatment and age significantly (P<.01) affected lipogenesis. Energy retention was significantly highest in birds housed under 16L:8D and lowest in birds housed under constant light throughout. Energy retention decreased with age and the effect of light treatment x age interaction was significant (P<.01).

Experiment 4

Light treatment significantly (P<.0001) affected gain and feed intake, but not gain/feed ratio (Table 8). Birds reared under 16L:8D performed better but this was not noticed until after third week when birds under constant light underwent depressed growth phase. When the study was terminated at 49 days of age, final body weights and feed consumed of chickens under 16L:8D regime were greater compared to birds reared under constant light.

Light treatment and age significantly (P<.05) affected the metabolic parameters measured (Table 9). Plasma T_3 concentrations were higher in birds housed under 16L:8D and declined with age regardless of light treatment. Plasma T_4 concentrations were uniformly higher in birds reared under 16L:8D and the levels increased with age. Light treatment x age interaction was found to be significant (P<.05) for plasma T_3 and T_4 concentrations. Lipogenesis was slightly higher in birds housed under 16L:8D and the rate of lipogenesis

TABLE 8

Effects of light treatment on body weight gain, feed consumed and feed efficiency[1-4]

Age,	Gain		Feed consumed		Feed efficiency	
wks	16L:8D	CL	16L:8D	CL	16L:8D	CL
	g		g		g/kg	
1	98	107	105	113	935	947
2	299	311	363	362	828	859
3	619	622	812	807	763	770
4	1248	1183	1441	1360	867	870
5	1425	1339	2234	2089	638	641
6	1841	1740	3116	2892	591	602
pSE[5]	27.0		57.3		23.5	

[1]Data are means of 4 groups of 6 male chicks each fed the experimental diet from day 1 to day 42 posthatching.

[2]For each variable except for feed efficiency the effect of photoperiod was significant ($P<.0001$).

[3]For each variable, the effect of age was significant ($P<0001$).

[4]Age x photoperiod interaction was significant ($P<.001$).

[5]pSE = Pooled standard error.

TABLE 9

Effect of light treatment on measures of energy metabolism and plasma T_3 and T_4 concentration in broilers

Variable	Light treatment	Age, wks 2	4	6	pSE[1]
Lipogenesis, dpm x 10^3.g liver·10 min[2,3] (starved and refed)	16L:8D	3.7	3.3	2.7	.21
	CL	3.2	2.3	2.3	
Lipogenesis, dpm x 10^3/g liver·10 min[2,3] (ad libitum feeding)	16L:8D	3.5	3.1	2.5	.20
	CL	3.1	2.1	2.1	
Energy retention, %[4,5]	16L:8D	53.4	45.0	39.0	2.44
	CL	43.6	39.7	31.1	
Plasma T_3, ng/ml[2,3]	16L:8D	2.84	2.40	1.42	.174
	CL	2.36	2.32	.87	
Plasma T_4, μg/dl[2,3]	16L:8D	21.6	34.2	53.9	2.71
	CL	18.2	31.5	42.6	

[1]pSE = Pooled standard error.
[2]Data are means of 6 chicks per age group.
[3]The age x light treatment interaction was significant ($P<.05$).
[4]Data are means of 4 groups of six chicks each per age group.
[5]The effects of age and light treatment were significant ($P<.001$).

decreased with age. The age x light treatment interaction significantly ($P<.05$) affected lipogenesis. Energy retention was higher in birds housed under 16L:8D. Energy retention decreased with age. Light treatment x age interaction significantly ($P<.05$) affected energy retention.

Discussion

Body growth curves are sigmoidal and the most rapid growth occurs early in life; the growth rate later slows to a plateau. Selection of parameters to measure growth is difficult due to this complexity.

It is likely that growth requires the presence of both GH and thyroid hormones (T_3 and T_4). These and other endocrine glands, including the endocrine pancreas and adrenal gland affect lipid, carbohydrate and protein metabolism. So any factor or factors that can suppress their secretion will effectively depress the growth rate. The growth-promoting effects of these are mediated, at least in part, via the somatomedins (insulin-like growth factors, IGF-I and IGF-II).

Thyroid hormones control skeletal muscle growth primarily by acting on protein synthesis. While low to intermediate levels of T_3 and T_4 are required for growth, high doses of T_3 and to a lesser extent T_4, will depress growth (May, 1980). A major aspect of the biological role of thyroid hormones results from a primary effect on the control of gene expression. White et al., (1978) reported that more than 100 enzymatic systems have been reported to be

a major role in supplying reducing equivalents (NADPH) for the support of fatty acid biosynthesis in the chick (Yeh and Leveille, 1969). Hepatic malic enzyme activity in the chick can be induced by thyroxine administration (Goodridge and Adelman, 1976).

Apart from photoperiod, diet affect the circulating concentration of metabolites and also that of hormones. For instance, fasting shifts glucose stores in the liver to the plasma and increases the circulating concentration of free fatty acids via an effect on lipolysis. In addition, muscle protein is likely to be broken down to generate amino acids for catabolism Growth hormone and corticosterone are likely to increase lipolysis. While GH will depress lipogenesis, corticosterone will increase the catabolism of protein, and a decrease in T_3 will reduce oxygen consumption and metabolism to preserve nutritional reserves. The rhythmic variation in concentrations of plasma T_3 and T_4 observed in this study are consistent with the view that feeding, stimulated by the onset of a light period resulted in an increase in the peripheral monodeiodination of T_4 and consequently, an increase in the levels of plasma T_3. Conversely, when feeding ceases at the onset of darkness, peripheral monodeiodination of T_4 decreases and the levels of plasma T_3 decrease. These studies are in agreement with Klandorf (1978) who suggested that in the chicken, the concentration of plasma T_3 and T_4 are regulated by different mechanisms. It is possible that the fall in plasma T_4 levels during the day when feeding starts is due to an inhibitory effect of increasing levels of plasma T_3 on

an unidentified component of the hypothalamo-pituitary-thyroid axis (Sharp and Klandorf, 1984).

In man and rats, the concentration of plasma thyrotropin (TSH) increases during the period of sleep (Fukunda et al., 1975) and it is possible that the increased concentration of plasma T_4 observed at the dark or early period in this study was due to a nocturnal increase in the secretion of TSH.

Pelham (1975) showed that melatonin was present in chicken serum during the dark period, but was usually undetectable during the light phase. Chickens treated with melatonin had reduced oxygen consumption and carbon dioxide production with anorexia, inactivity, and sleep lasting approximately 3h. (Bermudez et al., 1983). Fasting and melatonin production occur during the dark phase, and both are associated with reduced metabolic rate.

Thyroid hormones are necessary for normal growth and development but little is known about how their effects are exerted (Bernal and Reteloff, 1977). No clear correlation between thyroid hormone concentration and growth rate of normal chickens has been identified. Thyroid hormones probably act by stimulating both protein synthesis and degradation with the greatest accretion of protein occurring during euthyroid conditions. Although T_3 directly stimulates growth and maturation of embryonic chick cartilage, there is little information concerning the role of the thyroid on posthatching cartilage and bone growth in the chicken. The width of the growth plate has been widely used to evaluate the growth in length (Ashing et al., 1968). However, the

widening of a growth cartilage is not always associated with stimulation of longitudinal bone growth (Harrison, 1967). Chai (1976) reported that selection for thyroid activity resulted in a positive correlated response in body size of mice and its secretions might act on some factors necessary for increased body weight gain.

Plasma glucose, triglyceride (TG), and plasma free fatty acid (PFFA) were lower during AM sampling time than during the PM sampling time. There was a smaller increase in the plasma glucose concentration of the birds reared under constant light. This may have been due to the stress of constant light and the fall in the total blood volume, which could have caused the release of catecholamine.

The combined effect of diet, and age on several blood parameters that have been implicated in the regulation of carbohydrate and lipid metabolism have been documented (Yeh and Leveille, 1969). They reported that an increase in the dietary protein level decreased the flow of substrate through glycolysis and increased the production of glucose from substrate that were formerly in the pathways leading to fat synthesis.

Rosebrough et al., (1985) reported that plasma glucose was uniform within each group of chickens at all intervals and plasma TG showed no diurnal variations in either younger or old chicks. This observation is contrary to the finding of Twiest and Smith (1970) who reported significantly higher plasma glucose levels during the light hours compared to dark hours when chicks were

fed ad libitum under a 12L:12D schedule which may be due to feed consumption. Chandrabose (1970) has shown that under the LD regime, food consumption reaches a maximum in the afternoon and drops to almost zero before the dark period starts. Chandrabose has also reported that chicks do eat a little just before the light period start.

The data of Oppenheimer et al., (1978) indicated that malic enzyme activity may support a relationship between T_3 level and hormone action at the cellular level. Thus, a depression in either T_3 binding or circulating level (as is the case in the present studies) would result in decreased enzyme activity and subsequently de novo lipogenesis. It should be cautioned that although malic enzyme may provide the necessary NADPH for lipogenesis, it does not necessarily indicate that the enzyme strictly regulates lipogenesis. A more plausible explanation is that malic enzyme activity reflects NADPH utilization and does not regulate fatty acid synthesis.

It has been reported that restricting the metabolizable energy intake (but not protein intake) by about 25% had little effect on hepatic lipogenic enzyme activity in the laying hen (Pearce et al., 1976). However, it has been reported that in immature pullets, liver weight, liver lipid content and lipogenic enzyme (ATP citrate lyase and malate dehydrogenase decarboxlating ($NADP^+$)) activities were increased in the birds restricted to 75% and 60% of the ad libitum feed intake (Balnave et al. 1979). Contrary to the results of Balnave et al. (1979), it was found in our present work that feed restriction reduced the rate of

hepatic lipogenesis. Similarly, this energy restriction had a significant effect on other metabolic parameters. These metabolic parameters included triglycerides, triiodothyronine (T_3), thyroxine (T_4), plasma free fatty acids (PFFA), plasma glucose, lipolysis and energy retention. The present results are in general agreement with the effect of feed restriction previously observed by Pearce et al., (1976; 1980; and 1984). There was a significant effect of sampling time on triglyceride, T_3 and PFFA but no significant effect of sampling time on either T_4 or glucose. These are in agreement with results of Pearce et al., (1984) who reported that there was no significant effect of feed restriction on glucose metabolism. Regardless of diet, constant light depressed all parameters examined except for plasma free fatty acids and lipolysis and these were consistent with those results obtained by Calabotta et al, (1983).

Plasma free fatty acid levels increased during fasting and returned to normal upon refeeding whereas plasma TG levels seemed to increase to normal upon refeeding. From these findings, liver is the major site of fatty acid biosynthesis and this rapid adaptation of lipogenesis is undoubtedly related to the rapid rate of food passage through the gastrointestinal tract of the chick. As a consequence of this rapid rate of feed passage, a postabsorptive state is attained within a relatively short period of time. It seems possible that free fatty acids might reduce fatty acid synthesis by competing for coenzyme A, thereby limiting its availability for citrate cleavage. The plasma TG level determined in the same group of chicks under the same conditions was high.

This is in contrast to observations in the rat showing plasma TG levels to decrease upon refeeding following a fast (Baker et al., 1968). The difference between these two species is undoubtedly related to the major sites of lipogenesis in the chick compared to that of rat. In the rat, adipose tissue is a primary site of fatty acid synthesis, whereas in the chick, liver is the principal lipogenic organ. In the chick, a stimulation of fatty acid synthesis in liver requires triglyceride release for transport of fatty acids to the adipose tissue. In the rat, on the other hand, refeeding following a fast would limit fatty acid release from the adipose tissue and thereby reduce the availability of fatty acids for triglyceride formation and release from liver. Thus, it is not surprising that the plasma triglyceride level is elevated upon refeeding in the chick rather than being depressed as in the rat.

Triglyceride is the main form of transport for fatty acids from the liver to peripheral tissues, and a high plasma triglyceride concentration appears to favor fat deposition. Since hepatic triglycerides are immediate precursors for plasma triglyceride (O'Hea and Leveille, 1969) and plasma triglycerides are being in turn immediate precursors of those in adipose tissue, our results emphasize the prominent role of the liver in the chicken. These results are in agreement with other results reported in the literature (Leveille et al., 1975, Saadoun and Leclercq, 1983). The results of this experiment seem to indicate a positive correlation between de novo liver lipogenesis and plasma triglyceride content. Leveille et al. (1975) reported that lipogenic enzyme activity lagged behind

hyperlipogenesis following refeeding. Rosebrough et al., (1985) demonstrated that cycles of starvation and refeeding produced lipogenic rates that were higher than ad libitum values regardless of protein level.

The efficiency of energy retention and utilization was affected by both light treatment and diet. Chickens reared under 16L:8D had a significantly higher energy retention and also were more efficient in utilizing energy than those reared under constant light.

It has been documented (Morrison and Leeson, 1978) that in chickens, poor energy utilization is associated with increased heat production and metabolic rate, whereas efficiency of energy utilization is well correlated with body growth and body weight gain (Proudman et al., 1970). Masic et al. (1974) reported that broilers consumed significantly more feed than layers and ate more meals and spent significantly less time in feeding activity. Similar reports were documented by Barbato et al. (1980) when comparing high and low weight lines of birds. Cherry and Siegel (1979) in a similar study demonstrated that food was digested and cleared at a faster rate in a high weight line of chickens.

Robbins (1981) reported that a heavy, rapidly growing breed is more efficient in energy retention. From his study, he determined that a heavy growing broiler breed was 15% more efficient in retaining ingested energy than a lighter, slower-growing breed. This difference in observed efficiency may be due to a lower maintenance energy requirement, a higher efficiency of energy

utilization above maintenance or both. The amount of energy utilization for maintenance/metabolism relative to $BW^{.75}$ increased as dietary ME was increased. It has been reported (Balnave and Jackson 1973) that efficiency of energy utilization declines as dietary concentration increases. The higher efficiency has also been observed in mice (Canolty and Koong, 1976). It was shown that selection for rapid post weaning growth rate in mice resulted in a greater increase in efficiency of energy utilization. This was not accompanied by significant changes in maintenance energy requirement but was due primarily to a higher efficiency of energy utilization for gain.

The results obtained in these studies show better growth rate and higher energy retention from birds maintained under 16L:8D regime. This may be due to less energy used by these groups of birds according to McDaniel et al. (1977) who reported similar results. Ota (1967) reported that there was about 25 percent less heat production from birds in the light period group. Thus, the higher efficiency of energy retention observed in birds under 16L:8D and those fed a high energy diet is primarily due to a much higher efficiency of energy utilization above maintenance.

Lin et al., (1979) reported that a major factor contributing to the higher energetic efficiency of genetically obese versus lean mice is a much lower maintenance energy requirement. However, it has been reported early (Deb et al., 1976) that obese Zucker rats were twice as efficient as their lean counterparts in retaining ingested energy. It has also been documented that the

differences in weights between fat line (FL) and lean line (LL) chicks was not due to differences in feed intake but to differences in metabolic utilization of energy (Leclercq and Saadoun, 1982). In another study by Saadoun and Leclercq (1987), differences were found in the rates of lipogenesis in both liver and carcass of FL and LL birds. FL chickens exhibited enhanced hepatic lipogenesis. All the above seems to account for the increased body weight of the heavy breeds. The results in these studies have demonstrated that photoperiod and diet have an effect on these parameters and other aspects of body metabolism in eliciting increase body weight gain.

General Discussion

An absence of a dinurnal light cycle disrupts the endogenous time clock(s) of the chicken. Constant light elicits a stress situation that stimulates adrenal activity, including adrenal hypertrophy and increased synthesis and release of adrenal hormone, particularly corticosterone. This photoperiodic effect is exerted by way of the eyes and/or the pineal gland (and in some cases, as in lower vertebrate forms, directly by way of light penetrating the skull) to the CNS, and hypothalamo-pituitary axis as shown in Figure 1. A sequential release of hypothalamic corticotropin releasing hormone (CRH) and pituitary adrenocorticotrophic hormone (ACTH) will in turn cause an adrenal

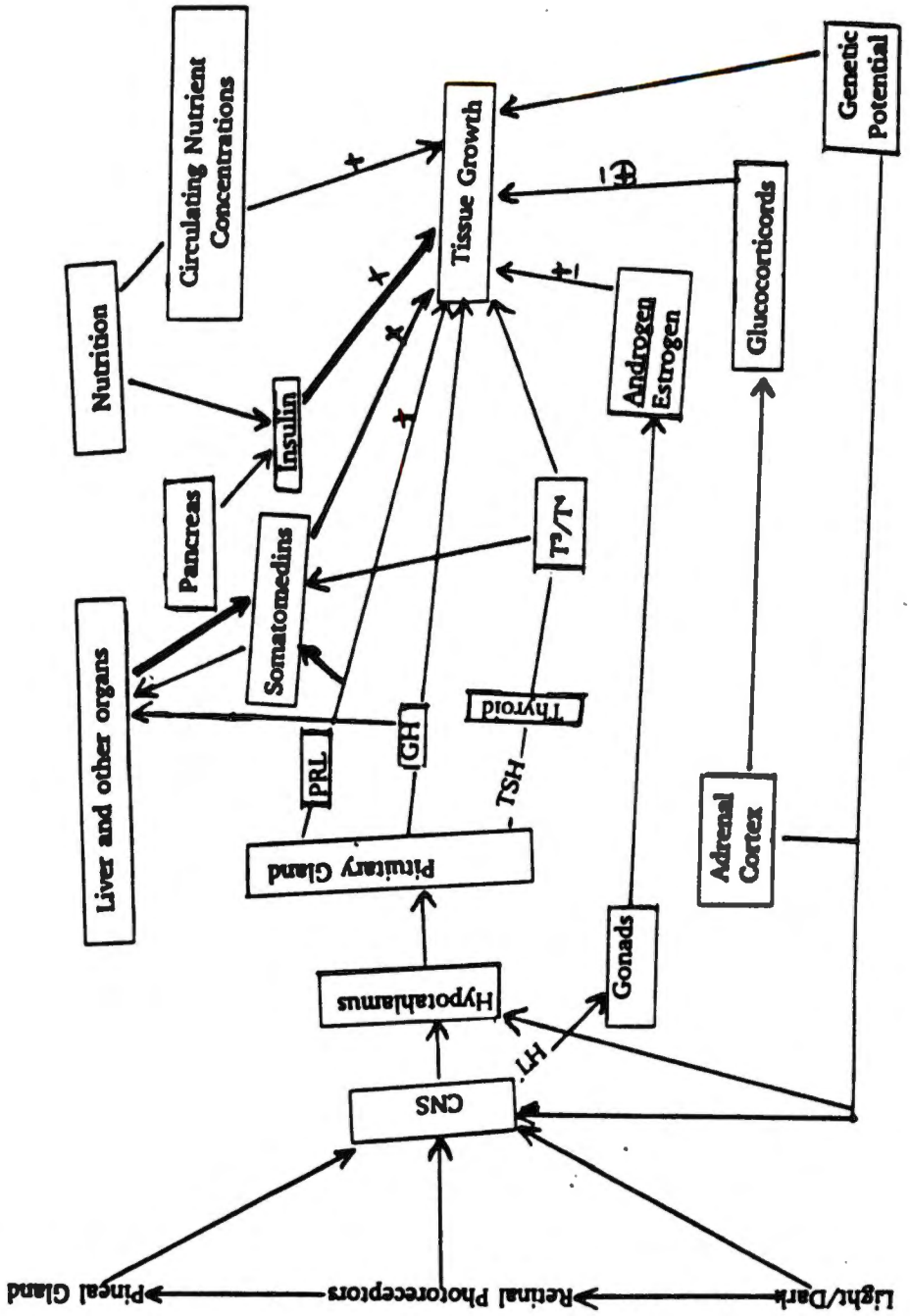

Figure 1: Environmental, Nutritional, Metabolic and Endocrine Interface.

hypersecretion of hormones. Fatranska (1971) reported that an abnormal lighting situation can trigger a hypersecretion of adrenal corticosteriod. Under Seyle's (1951) General Adaptation Syndrome, stress situations induce a hyperactivity of adrenal glands under a preceding stimulation by hypothalamic CRH and ACTH. Indeed, under stress the corticoid levels in chicken plasma have been reported to show up to a fourfold increase (Buckland et al., 1976).

The hypothalamus exerts a dual control of growth hormone (GH) secretion; hypophysiotropic factors (releasing factors) either stimulate or inhibit GH release. There are two hypothalamic factors stimulating GH secretion in the domestic fowl. These are the modified tripeptide, thyrotropin releasing hormone (TRH) and a growth hormone releasing factor (GRF). It is often presumed that GH, thyroid hormones and others act on growth through an intermediary factor or factors, the somatomedins. The somatomedins have been chemically characterized as two entities: insulin-like growth factor 1(1GFI) and 1GFII. The liver has been established as the most likely major source of somatomedin(s) production. Hence, anything that can cause depression of somatomedin(s) will effectively decrease the level of these growth hormones, since the effects of these hormones are medieated at least in part by avian somatomedin(s). The somatomedins are probably transported in the plasma in association with a binding protein whose syntheses also probably is GH dependent and glucocorticoid controlled.

Growth hormone in birds act synergistically with glucagon, even though the latter hormone encourages glycogenolysis and hyperglycemia. Simultaneously, growth hormones act on lipid metabolism by stimulating lipolysis, inhibiting lipogenesis in the liver and increase glucose uptake by adipose tissue. Lipolysis provides noncarbohydrate fuel, which in turn spares carbohydrate substrates, thus reinforcing the hyperglycemia initiated by increased gluconeogenic enzyme activity. Glucocorticoids appear to have a catabolic role in birds. It causes a decrease in nitrogen balance and an increase in nitrogen and urinary uric acid excretion in glucocorticoid treated chickens (Adams, 1968).

It is therefore likely that the reduction or depression in growth rate observed in birds reared under constant light was due to an increase in endogenous corticosterone which directly depresses the circulating concentration of somatomedins and indirectly depresses growth hormones plus other metabolic parameters. Moreover, it is likely that increased secretion of glucocorticoid exerts a direct catabolic effect on the muscles, favoring protein degradation over synthesis. As protein catabolism increases and glucogenic amino acids are converted de novo to carbohydrate substrates, nitrogen excretion increases, weight decreases and all these will lead to a decrease in energy retention and a reduction in body weight. All of these effects are brought about by ACTH release, particularly over a prolonged period of time as in chronic stressful situation of constant light. Due to this, it might be

speculated that the reduction of the body weight of birds reared under constant light is mediated by glucocorticoids which depress somatomedin(s) production.

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PART IV

SUMMARY AND CONCLUSION

Summary and Conclusion

Attempts were made in this study to determine the role of photoperiod, sex and energy restriction and their interactions on energy metabolism in broiler chickens.

Series of experiments were conducted to obtain information on the effects of photoperiod, sex and energy restriction and their interactions on body weight gain, feed consumption, feed efficiency, energy utilization, and several metabolic parameters associated with energy metabolism, viz, hepatic lipogenesis, rate of lipolysis using abdominal fat pad explants, energy retention, plasma concentrations of T_3, T_4, PFFA, TG and blood glucose levels.

It was found that diet, sex and light treatment affect body growth and energetic efficiency. Constant light and low energy diets were determined to significantly depress feed efficiency and body growth. The results obtained in these experiments show that the accepted practice of using constant lighting may not be the best lighting regime for growing broiler chickens. Birds under 16L:8D regime and those fed high energy diet retained and utilized energy above maintenance much more efficiency than their constant light and low energy fed counterparts. The energy retention was significantly lower in birds housed under constant light and those fed low energy diets.

Constant light depressed all metabolic parameter measured except for plasma free fatty acids and rates of lipolysis which were higher under constant

light. The poor or reduced weight of birds reared under constant light was attributed to ACTH released due to stressful situation of constant light and the depression in somatomedin production, thereby reducing availability of growth hormone in the body.

These studies seem to indicate that combining photoperiod with high dietary energy and restricted feeding will result in a substantial and significant improvement in overall performance of broilers. In addition, the use of photoperiod offers a saving in the amount of electrical energy used for rearing broiler chickens.

VITA

Hammed Akande Olanrewaju was born January 1, 1955 in Gbongan, Oyo State, Nigeria. In December 1972, he graduated from Iree Baptist High School. He obtained an Ordinary National Diploma in Animal Health and Husbandry from the University of Ife, Institute of Agricultural Research and Training, Nigeria in July 1977. He worked as Livestock Assistant in Ministry of Agriculture and Natural Resources in Oyo State of Nigeria. He received a Bachelor of Science degree in Animal and Poultry Sciences from Tuskegee University, Tuskegee, Alabama, USA in July 1981. He immediately continued his education at the same university where he earned a Master of Science degree in Animal and Poultry Sciences (Nutrition) in May 1982. He returned to Nigeria immediately to serve Federal Government of Nigeria under National Youth Service Corps and at the same time got married. He enrolled in the Graduate School of the University of Tennessee, Knoxville in January, 1987 and he received a Doctor of Philosophy degree in Animal Science with concentration in Nutrition in May 1990.