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UNIVERSITY OF ALBERTA

PHOTOPERIOD INFLUENCES ON THE SEASONAL ENERGY METABOLISM OF EWES

by

VALOREE ANN WALKER ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

ANIMAL PHYSIOLOGY

DEPARTMENT OF ANIMAL SCIENCE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled PHOTOPERIOD INFLUENCES ON THE SEASONAL ENERGY METABOLISM OF EWES submitted by VALOREE ANN WALKER in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in ANIMAL PHYSIOLOGY.

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ABSTRACT

Photoperiodic influences on seasonal variations in energy metabolism was examined in 24 Suffolk ewes. The ewes (6 per group) were subjected to one of four light regimens; A) constant 12L:12D; B) a sinusoidal pattern of artificial photoperiod, the reverse of the natural seasonal photoperiod; C) a sinusoidal pattern of artificial photoperiod, closely mimicking natural seasonal photoperiod and D) natural seasonal photoperiod experienced at 53.5°N latitude. Artificial summer and winter 'solstices' were 18L:6D and 6L:18D, respectively.

For 76 weeks, a constant near-maintenance feeding regimen was imposed, to examine metabolic heat production (MHp), thyroid hormones, and progesterone, and relationships independent of changes in food intake. Following the near-maintenance feeding period, the ewes were fed *ad libitum* for a further 32 weeks, to examine photoperiod influences on voluntary food intake and the relationship to MHp patterns.

A significant ($P<0.05$) sinusoidal pattern for MHp and thyroid hormone concentrations was evident for ewes exposed to a seasonal light patterns, with thyroid patterns closely paralleling MHp. The timing of the onset and termination of reproductive patterns, as indicated by plasma progesterone concentrations, were closely regulated by the seasonal light patterns imposed. Termination of estrous cycles coincided with elevated plasma thyroid levels, and increases in MHp.

Ad libitum feeding resulted in an initial increase in intake for all groups irrespective of light regimen. Significant differences ($P<0.05$) in voluntary food intake were observed following 20 weeks of *ad libitum* feeding, with intake greatest for ewes exposed to long daylengths. During this phase MHp was closely correlated ($r^2 = 0.93$, $P<0.001$) with food intake.

Differences in physical activity of the ewes examined during the final 12 weeks of restrict feeding and throughout the *ad libitum* feeding period, did not appear to contribute to the photoperiod induced changes in MHp.

Seasonal photoperiod was responsible for cuing changes in MHp, the physiological mechanism of which was likely through changes in thyroid activity.

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I. INTRODUCTION

A. Animal-environment interactions

It is a common perception that animals possess biological clocks. Numerous animal species respond physiologically and behaviorally in a regular repeatable manner in relation to their environments. These environmentally related rhythms fall into a classification of clock-like biological processes which may be circadian (daily), tidal, lunar-monthly or circannual (Brady, 1982).

Circannual biological rhythms are usually linked to climatic variables which change seasonally. The physiological and behavioral modifications are often adaptive alterations in anticipation of the forthcoming season. Prominent examples of these include the initiation and termination of reproductive function, the moult of skin, fur and plumage, migratory behavior and hibernation (Pévet, 1986). Environmental variables known to induce and regulate many biological rhythms include temperature, rainfall, photoperiod, food quality and availability (Pévet, 1986). The degree to which these individual variables change annually, and often the degree to which they influence animals is dependent on the geographical location in question.

Under natural conditions, animals are never subjected to one single environmental factor and there is normally an interactive influence of factors at any time. However some variables are more accurate indicators of subsequent seasonal changes than others and are often the primary cues initiating responses in the animal.

In tropical and equatorial regions of the world in which the fauna is immensely rich in species, more irregularly recurring external cues such as rainfall are utilized for the timing of physiological functions (Pévet, 1986). In temperate and polar regions both temperature and photoperiod (daylength) change in a regular manner annually. However, daylength is the most exact seasonal indicator and provides a reliable signal for the time of year.

B. Seasonal Photoperiodism

Photoperiod has been unequivocally shown to be a primary cue in the timing of annual reproductive capability in many mammalian (Reiter, 1986) and avian species (Nicholls et al., 1988). Mammalian species shown to have photoperiodically regulated reproductive activity include several breeds of domesticated sheep and various wild species including ferrets, mink and voles (Sadleir, 1969). Seasonal photoperiod has also been shown to influence directly or indirectly other physiological functions. The growth rate of domestic cattle and sheep under controlled lighting situations, increases with exposure to fixed daylengths of 16 h vs 8 h, under conditions of restricted feeding (Tucker and Ringer, 1982). Other mammals display distinct appetite cycles which are induced by seasonal photoperiod but unrelated to the feed quantity available (Kay, 1985). In an experiment in which red deer (*Cervus elaphus*), Soay and Suffolk x (Finn x Dorset) cross sheep were subjected to a cycle of daylength changes of normal amplitude but of 6 month duration over a two year study period, variations in voluntary food intake followed the 6 month light cycle (Kay, 1979). This response was more marked in the red deer and more primitive Soay sheep than in the domestic sheep (Kay, 1979).

There is also evidence that humans may respond to changes in seasonal photoperiod. Recent studies have shown that a condition arising in some individuals, known as seasonal affective disorder (SAD), is causally linked to the amount of daily light experienced (Rosenthal et al., 1986). This condition arises in the fall and winter months and symptoms include depression, fatigue, lethargy, excessive sleep and carbohydrate craving. Effective treatment has involved the exposure of individuals to 5 to 6 hours daily, of bright (2500 lux) full spectrum lights, lengthening the daylight artificially during the naturally short photoperiod. The symptoms are found to disappear during spring and summer and individuals may have periods of euthymia or hypomania at this time (Rosenthal et al., 1986).

The ability of animals to respond physiologically or behaviorally to seasonal light:dark (L:D) changes is referred to as photoperiodism (Brady, 1982). The mechanism by which light information is sensed in mammals occurs via the retina and a complex pathway of neural signals are sent to the pineal gland which then transduces the information into chemical signals (Pévet, 1986). The pineal hormone melatonin has been implicated in the regulation of various circannual physiological processes (Cassone, 1990), although its output is utilized in different ways by various species (Kennaway, 1984). The neurohormonal mechanisms involved in the photoperiodic control of physiological responses are described in more detail by Kay (1985), Pévet (1986) and Cassone (1990). An adaptation of a schematic diagram of photoperiodic influence on physiological parameters (Kay, 1985) is shown in Figure I.1. Photoperiodic influences on certain rhythmic physiological processes such as reproduction have been conclusively shown but the degree to which photoperiod influences other processes and the mechanism by which these responses occurs are still uncertain. The physiological pathways of interest and the central focus of the current study are shown by the wide arrows in Figure I.1.

C. Seasonal energy metabolism

A seasonal rhythm has been demonstrated in the energy metabolism of a number of mammals. White-tailed deer (Silver et al., 1969; Moen, 1978), moose (Regelin et al., 1985; Renecker and Hudson, 1986), roe deer (Weiner, 1977) and domestic sheep (Blaxter and Boyne, 1982) have been shown to exhibit a seasonal pattern in metabolic heat production (MHp) involving a decrease in the fall and winter and an increase in the spring and summer seasons. However, the degree of variation (amplitude of the cycles) differs greatly between species.

The variations observed may be related to species differences but also to other parameters intrinsic or extrinsic to the animal, such as the quantity of food consumed or ambient temperature. Furthermore, some studies conducted, examining the seasonal patterns in energy metabolism, have been confounded by the influence of the interaction of environmental parameters, including photoperiod, temperature and nutrient intake, on the animals. It is only through the examination of each environmental factor individually, that the direct extent to which that factor influences animal metabolism can be determined.

Ambient temperature has been shown to have direct effects on the MHp of a number of species. Controlled environmental studies involving domesticated sheep and cattle have shown that with prolonged exposure to low ambient temperatures there is an increase in MHp (Christopherson and Young, 1986). Domesticated sheep establish a higher thermoneutral resting MHp when acclimatized to the outdoor winter environment or when acclimated to cold in controlled environment chambers (Christopherson and Young, 1986). The experimental results of the effects of ambient temperature on MHp in domestic species appear contradictory to the observed natural seasonal pattern of a decrease in MHp during fall and winter; the period of lowest ambient temperature. Comparisons of the above findings to a natural situation may not always be valid. Controlled studies often involve restricted feeding, alteration of external covering (shorn sheep) and reduction of the ability to utilize behavioral strategies. As mentioned, many other factors must be considered in a natural environmental situation, such as body condition of the animal (thermal insulation), and behavioral strategies (shelter seeking and utilization of solar radiation for warmth). Behavioral changes in white-tailed deer have been observed by Moen (1974) whereby in outdoor winter situations deer become lethargic compared to those confined to chambers which exhibit a more traditional cold-induced response. Unlike laboratory findings the temperature-metabolism relationships in a more natural environment situation have shown that metabolic rate is reduced in the winter, in a number of wild ungulates, including bison, elk, moose and bighorn sheep (Parker and Robbins, 1985). This suggests that some other environmental parameter may be directly influencing the seasonal rhythm in MHp.

Research has been conducted on the influence of food intake on MHp. Changes in the level of intake result in changes in MHp as diet induced thermogenesis varies (Kay, 1985). A seasonal cycle in voluntary food intake has been observed in ruminants with examples including some breeds of domestic sheep (Gordon, 1964; Greenhalgh and Reid, 1974; Blaxter et al., 1982), red deer (Milne et al., 1978), reindeer and caribou (McEwan and Whitehead, 1970; Ryg and Jacobsen, 1982). This seasonal cycle in appetite is coincident with the seasonal rhythm in MHp with increases in the spring/summer and decreases in fall/winter (Silver et al., 1969, Blaxter and Boyne, 1982). Studies on sheep and deer have shown that the cycle in appetite is entrained by seasonal changes in photoperiod (Simpson et al., 1984). Simpson and colleagues (1984) exposed Suffolk x (Finn x Dorset) sheep and red deer to an artificial photoperiod of two annual cycles of daylength in one calender year. This resulted in two distinct cycles of food intake in response to the daylength.

The seasonal change in MHp have been associated with and often attributed to the seasonal pattern in food intake. Conversely seasonal patterns in MHp were observed while the effect of food intake was supposedly removed (Blaxter and Boyne, 1982). This prompted them to hypothesize that voluntary food intake may be associated with variations in basal metabolic rate. In their experiment Blaxter and Boyne (1982), analyzed heat production data of domestic sheep collected from feed evaluation trials (fed at about maintenance level of nutrition). Although changes in metabolism were coincident with season whereby maximum MHp occurred in spring/summer and minimum MHp occurred in winter months, they were unable to state conclusively that daylength was the primary factor. The sheep had been housed in metabolism cages in a large windowed room thereby implicating that daylength may be a conditioning factor (Blaxter and Boyne, 1982). Findings of a seasonal pattern in energy metabolism lends support to the idea that the observed photoperiodic regulation of food intake may actually be a reflection of photoperiodic control at a different physiological level. The question still remains therefore, as to the direct influence of seasonal photoperiod variations on energy metabolism.

D. Approach and Thesis organization

The overall purpose of the study was to determine if seasonal photoperiod has a direct influence on energy metabolism (based on heat production values). The hypothesis was tested utilizing a domestic breed of sheep (Suffolk) known to possess reproductive and appetite cycles regulated by seasonal photoperiod. To evaluate the mechanism of possible photoperiodic influence, other physiological parameters were examined including associated hormonal changes and behavioral responses.

The study focused on the following:

1) The determination of the influence of artificial and natural seasonal photoperiods and constant photoperiod on the MHp of ewes with all other environmental parameters kept as near as possible constant.

2) The examination of seasonal changes in hormone levels:

  i) progesterone (P4): used as an index of reproductive activity to evaluate if the experimental light treatments utilized elicited a photoperiodic response in the test animals ie., was the photoperiod cue received by the ewes?

  ii) thyroid hormones: total and free triiodothyronine (T3) and thyroxine (T4) which are known to be related to MHp responses, and as such, may provide evidence of a hormonal response elicited by photoperiodic change.

3) The examination of photoperiodic influences on the voluntary food intake and its relation to MHp.

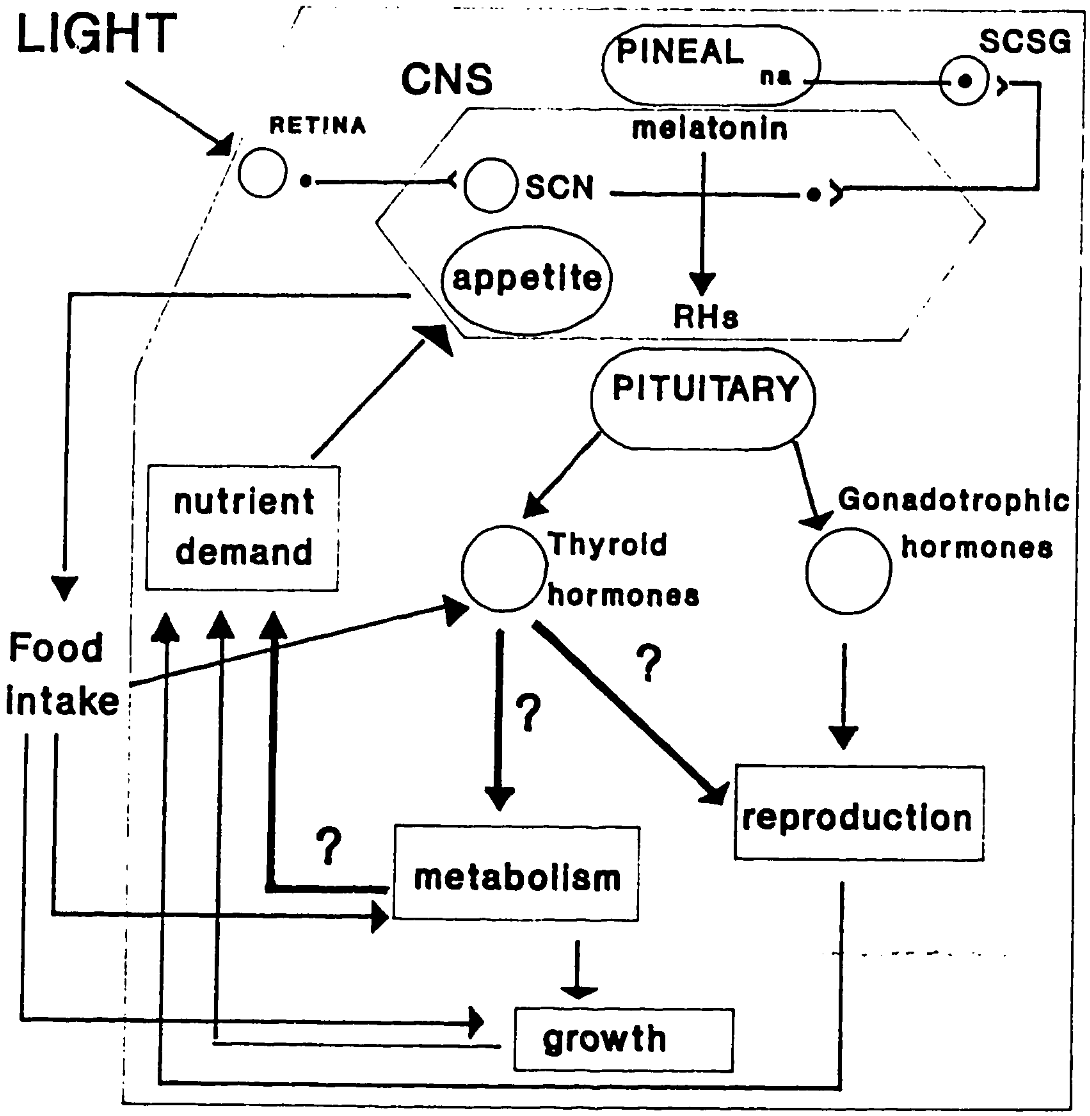
4) The assessment of behavior of the sheep in relation to photoperiod as indicated by daily activities including standing/lying, head movements, jaw movements and rumination time.

The total time frame of the study was 129 weeks. The first 94 weeks involved near-maintenance feeding, with the initial 18 weeks adjustment to the diet and experimental conditions at which time all the ewes in an artificial light pattern were exposed to a constant 12L:12D. During the remaining 76 weeks, the ewes were exposed to their respective light treatments and measurements were taken of MHp (chapter II), thyroid hormone concentrations (chapter III) and progesterone concentrations (chapter IV). Week 95 and 96 of the trial was the transition period whereby ewes were gradually offered increasing amounts of feed leading to *ad libitum* feeding for the remaining 33 weeks (chapter V). Chapter IV describes measurements of physical activity taken during weeks 72 to 129 overlapping the restrict and *ad libitum* feeding periods.

The timing of metabolic, endocrine, reproductive and behavioural patterns were evaluated in relation to photoperiodic treatment patterns. The understanding of the integration of physiological changes elicited by seasonal photoperiod may help to explain their adaptive significance.

Figure I.1

Schematic of photoperiod influences on physiological parameters, adapted from Kay (1985), with wide arrows representing the focal points of the present study.



SCN - suprachiasmatic nucleus
SCSG - superior cervical sympathetic ganglion
RHs- releasing hormones from hypothalamus
na - noradrenaline

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II. INFLUENCE OF PHOTOPERIOD ON THE METABOLIC HEAT PRODUCTION OF EWES

INTRODUCTION

Pronounced seasonal variations occur in the energy metabolism of both wild and domestic ungulates. An annual cyclic pattern in energy metabolism with an increase in spring and summer and decrease in winter have been reported for moose (Regelin et al., 1985; Renecker and Hudson, 1986), reindeer (Nilssen et al., 1984), white-tailed deer (Silver et al., 1969; Holter et al. 1977), roe deer (Weiner, 1977) and domestic sheep (Blaxter and Boyne, 1982; Argo and Smith, 1983).

This variation in metabolism has been attributed to seasonal changes in ambient temperature, food availability, and other environmental variables (Kay, 1985). In controlled temperature studies, with exposure to acute cold, an animal responds with an immediate increase in heat production to maintain homeothermy. Prolonged chronic exposure to low ambient temperatures induces an upward adjustment of thermoneutral resting metabolic rate (Young, 1975). This typical laboratory response is contradictory to the natural seasonal metabolic pattern in which energy metabolism decreases at a time when environmental temperatures are also decreasing.

For sheep and deer a natural seasonal pattern in voluntary food intake has been reported, with a maximum in the spring and summer and a marked decrease in winter (Gordon, 1964; Milne et al., 1978; Kay, 1979). Seasonal changes in appetite is an apparent adaptive response related to the natural abundance of food in the summer and often a scarcity in winter. However, changes in intake are not strictly due to food availability, but have been shown to be influenced by changes in daylength (Kay, 1979; Argo and Smith, 1983). Simpson et al. (1984), showed that under conditions where food was provided *ad libitum* and a seasonal photoperiodic regimen imposed involving two cycles of daylength change in one year, two distinct cycles of food intake resulted for both deer and domestic sheep.

It is well established that food intake has a direct effect on the rate of energy metabolism (Blaxter, 1962). Blaxter and Boyne (1982) however, deduced from examination of data from a feed evaluation study, that the seasonal variation observed in heat production by sheep was not due to changes in feed intake. Their data were derived from measurements of animals housed in a windowed building, and fed near maintenance rations. Blaxter and Boyne (1982) suggested that there was a seasonal component of metabolism independent of feed intake and suggested that daylength may be involved.

Seasonal photoperiod has a precise and repeatable annual pattern in temperate and polar regions and has been shown to serve as an important cue for the timing of the onset and termination of reproductive activity in sheep (Yeates, 1949). There is no direct evidence that seasonal changes in energy metabolism are cued directly by photoperiod nor is it clear whether these are simply related to the natural seasonal changes in food intake. The aim of this study was to determine if seasonal photoperiod has a direct influence on energy metabolism when other influencing factors are held constant.

MATERIALS AND METHODS

Animals, Housing and Management

The study was conducted at Edmonton, Alberta, Canada located at 53.5° N latitude. Twenty-four Suffolk ewes born in January and February of 1987, were utilized in the experiment. The ewes were caged in metabolic crates to facilitate individual feeding and fecal collection. The ewes were randomly allocated to one of four temperature-controlled rooms, three of which were windowless. Ceiling-mounted fluorescent tubes were utilized, giving cool white illumination. Light intensity was measured with a Spectra-Combi 500 light meter, sensitive to 35 lux. The internal lighting of the rooms at the level of the animals' head was between 1100 and 1200 lux. All rooms were continuously ventilated and temperature was maintained at 20.5 ± 2.4°C.

Throughout the trial, a constant near-maintenance ration, was fed at 1400 daily. This ration was formulated to meet the requirements of a 50 kg ewe (NRC, 1986). The daily feed allocation consisted of 600 g pelleted barley based concentrate and 200 g chopped brome/alfalfa mixed hay. The metabolizable energy and crude protein of the pellets and hay on a dry matter basis were 12 MJ/kg, 15% and 9 MJ/kg, 12%, respectively. The sheep had *ad libitum* access to water and trace-mineralized salt throughout the experiment.

Experimental Design

Initially 18 of the ewes, 4 to 5 months of age, were maintained in the experimental facility and exposed to constant daily 12 h light, 12 h dark (12L:12D), for 18 weeks. Following this constant light period, the sheep were randomly assigned to one of three artificial light treatments for the next 76 weeks. An additional group of six ewes (treatment Group D) were brought into the experiment from the natural outdoor light environment, 5 weeks prior to the start of the artificial light treatments. This group continued to be exposed to the natural light pattern in a windowed room where light intensity varied daily depending on season and weather conditions.

The light treatments were as shown in Figure II.1: Group A, constant 12L:12D; Group B, a sinusoidal pattern of light change in reverse to that of natural light, involving an initial increase in daily light; Group C, a sinusoidal pattern of light change closely mimicking the natural light pattern, involving an initial decrease in daily light; and Group D, natural light (windowed room). The artificial summer and winter 'solstices' were 18L:6D and 6L:18D, respectively. For the artificial light regimens, the lights were regulated daily by automatic timers whose time settings were adjusted manually each week.

Experimental Measures

Measurements of resting metabolic heat production (MHp) were taken every 4 weeks, on each sheep, using the waterbath procedure described by Young et al., (1988). To avoid disruption of the daily feeding routine and confounding effects of feeding on MHp, all measurements were performed 16 to 18 hours postprandial. Resting metabolic rate (MHp) was calculated from rate of outflow ventilation (V_o) from the face mask (approx. 110 l/min) and input and output oxygen concentrations (O_i and O_o, respectively) using the equation of McLean (1972).

$$MHp = 20.47\ V_o\ (O_i - O_o)$$

Oxygen concentrations were measured using a dual-channel paramagnetic analyzer (Taylor Servomex OA 184). These data were recorded and stored for later processing and analysis using an electronic Datataker (model DT100, Data Electronics, Box Hill, Vic., Australia). The system was calibrated every 4 weeks using the iron burner technique of Young et al (1984).

Fecal collections were conducted every 12 weeks over the 76 week period for determination of dry matter (DM) digestibility. The ewes were weighed biweekly utilizing scales accurate to ± 1 kg. Values 2 weeks following each shearing period (post-shearing live weight) were utilized in the statistical analyses, to remove the effects of shearing on live weight. The ewes were shorn approximately every 12 weeks to facilitate MHp measurements and for the measurement of wool growth.

Statistical Analyses

Analysis of variance was performed using the General Linear Models (GLM) procedure (SAS, 1988), for DM digestibility, post-shearing live weight, weight gain and wool growth. Treatment differences were established using the error term of sheep nested within treatments. Treatment differences for DM digestibility, live weight and wool growth were determined using a t-test equivalent to Fisher's least significance difference (LSD) test (SAS, 1988).

Two methods were utilized to evaluate the functional response of MHp to photoperiod, these being 1) polynomial regression analysis and 2) periodic regression analysis. A process of polynomial curve fitting (fifth degree, quintic equation) was initially done to examine the patterns of MHp and to provide an estimate of the time of maximum and minimum MHp values from visual appraisal of graphs and fitted values. The computed peak values and time of these peaks for each of the above were subsequently compared by t-test.

Further analysis of the relationship between MHp and the annual light cycle were made using the procedure for a periodic curve as outlined by Little and Hills (1978). To each set of data from an individual ewe and for each treatment group, the following equation for a periodic curve was fitted:

$$Y = a_0 + a_1 \cos C X + b_1 \sin C X$$

where X was time in weeks from the imposition of the treatments, and C was the constant equal to 360° divided by the number of weeks in a cycle. The initial analysis utilized a 52 week cycle ($C=6.923$). Further analysis was conducted to examine possible cycle lengths between 30 and 70 weeks. The term a_0 was defined by the weighted mean heat production value around which the wave fluctuated. The amplitude of the wave was calculated from two times the square root of $a_1^2 + b_1^2$. The point in the cycle where the wave reached its maximum value is referred to as the phase angle and was computed from the arc tan of b_1/a_1 (θ'), converted to angles. Phase angles (θ) were computed using the rules outlined by Little and Hills (1978), whereby if b_1 was positive and a_1 positive $\theta=\theta'$; if b_1 was positive and a_1 negative $\theta=180°-\theta'$; if b_1 was negative and a_1 negative $\theta=180°+\theta'$; and if b_1 was negative and a_1 positive $\theta=360°-\theta'$. These calculations were also computed for the different seasonal light patterns utilized as well as for the pattern of MHp. The difference between the phase angles of the heat production and light treatments provided an estimate of the phase delay or response time of metabolism to light changes.

Analysis of variance, using the General Linear Models procedure (SAS, 1988), was used to compare the computed amplitudes and phase delays. Mean differences were determined using a t-test equivalent to Fisher's LSD test. Unless otherwise specified all values are expressed as means ± standard deviation (SD) and significance was assessed at $P < 0.05$.

RESULTS

One ewe from Group A, (#239) was a replacement brought into the experiment 4 weeks into exposure to the 12L:12D period, and had been exposed previously to natural light conditions. Three additional ewes, two from Group C and one from Group D, were removed during the course of the experiment for reasons unrelated to the experimental treatments and were not replaced. Data from these ewes were not included in the statistical analysis of MHp.

The temperature in the rooms remained relatively constant, and the light patterns resulted in designed treatment curves which were found to have no consistent influence on changes in DM digestibility of the feed, live weight, weight gain or wool weight. Average values for each parameter are shown in Table II.1. Treatment differences in weight gain were only evident during the final 20 weeks of the trial, such that groups C and D had a significantly greater gain than group B (Table II.1). The estimated weight gains for each group are shown in Figure II.1. The ewes in Group A were significantly heavier than those in any other group during the final 20 weeks, with the exception of one ewe in the same group which had recurrent periods of bloat and inappetence throughout the study and was therefore not included in the live weight mean (Table II.1). Similarly the average weekly wool growth was significantly greater for Group A (Table II.1).

Polynomial analysis of resting metabolic heat production

Figure II.2 illustrates the average MHp pattern derived from polynomial smoothing of the resting MHp values and the observed MHp values of the four treatment groups. A distinct cyclic pattern in MHp was evident for the ewes in Groups B, C and D, with a maximum value occurring during exposure to an increasing daylength and minimum value occurring during exposure to a decreasing daylength. A similar pattern but of significantly lower amplitude was observed for ewes in Group A. The results for each ewe show that MHp changed in a curvilinear manner similar to the light pattern with the regressions being statistically significant for 13 of 15 ewes in a seasonal light pattern and 2 of 6 ewes in constant light (Table II.2).

The calculated maximum and minimum average resting MHp values (watts and watts/kg$^{.75}$) for the ewes in each light treatment are shown in Table II.1. For the ewes in seasonal light there was a difference between the maximum and minimum MHp (W/kg$^{.75}$) of approximately 26% while the sheep in constant light (group A), had a difference of only 11%. Group D had a significantly greater difference between maximum and minimum MHp/kg$^{.75}$ (33%) than the other groups. Similarly the average maximum heat production value per kg$^{.75}$ was significantly higher for group D in comparison to the other groups.

As shown in Table II.1, the minimum MHp value for Group A occurred after approximately 59 weeks of exposure to constant 12h daily light, while maximum values occurred after 84 weeks. The timing of the onset of maximum and minimum MHp were opposite for group B and C which were exposed to reverse artificial sinusoidal light patterns but occurred 13.6 ± 2.1 and 14.3 ± 3.4 weeks following the week of the shortest and longest daylength, respectively. Similarly Group D, in natural light exhibited a maximum MHp after 15.5 ± 2.9 weeks after the shortest day and a minimum after 18.5 ± 3.3 weeks after the longest day.

Fitting periodic curves to MHp values

A sinusoidal pattern in MHp was clearly evident for ewes exposed to each photoperiodic regimen as shown by the fitted periodic curves for each ewe in Figure II.3. Table II.3 summarizes the results of this regression analysis for resting MHp using Little and Hills' equation, for a 52 week cycle, and a total of 20 heat production values for each ewe collected over a 71 week period. Generally, the pattern in MHp followed a 52 week cycle with 14 of 15 calculated regressions being significant for ewes exposed to a seasonal light pattern, whilst only one of the six calculated regressions were significant for the ewes kept in constant light. Again when the same analysis was conducted utilizing values (n=15 observations/sheep) from the final 52 weeks of the study (Table II.4), versus 71 weeks, 13 of 15 regressions were significant for the ewes in seasonal light while none were significant for those in constant light.

When the analysis was repeated considering variations in the length of the cycle from 52 weeks, significance ($P<0.02$) was observed for three additional sheep in group A with cycle lengths of 64, 68 and 76 weeks. This cycle length was significantly longer than that of the other groups in which the lowest standard error of the estimate was obtained utilizing a cycle length of 50.2 ± 3.4 weeks.

The mean amplitude of the sine function for group D (18.3 watts) was significantly greater than group A (8.7 watts), this being a difference of 110%. Groups B and C had an intermediate value for the mean amplitude (13.6 ± 5.9 watts) which was approximately 56% greater than group A (Table II.4). The amplitudes determined for the three sheep having significant patterns of extended cycle lengths (group A) were 8.6, 12.6 and 13.2 watts.

The groups exposed to seasonally changing light reached a maximum MHp 15.1 ± 3.2 weeks after the shortest day. Maximum MHp values for the group in constant light were out of phase with the natural photoperiod group, and when calculated in relation to the natural seasonal light pattern, occurred -3.8 ± 1.5 weeks in relation to the natural shortest day.

DISCUSSION

The distinct pattern in metabolic heat production (MHp) observed for the ewes exposed to a 52 week seasonal light pattern, clearly indicates that the annual pattern of changing daylength does influence MHp, and therefore influences, whole-animal energy metabolism. Evidence of direct response to light was further validated by the reproductive response discussed in a subsequent chapter (IV). Exposure of the animals to a reverse seasonal pattern of daylength resulted in a reverse seasonal cycle of MHp. The general pattern observed involved an increase and decrease in MHp with exposure to increasing and decreasing daylengths, respectively. Natural light had a greater influence on the degree of this response, than did a similar pattern of artificial light, as evidence by the greater amplitude of group D.

Both the polynomial and periodic curve fitting analysis gave similar patterns confirming the presence of a consistent rhythm in MHp. In the polynomial analysis the time intervals are not fixed as opposed to the periodic analysis when it was initially fixed at 52 weeks. The polynomial analysis provided more flexibility and allowed for curves of varying shapes (amplitudes) and sizes (duration). The polynomial analysis initially was conducted to determine the presence or absence of a significant curvilinear response in the MHp data, and provided higher coefficients of determination (R^2) than the periodic analysis, as it took into consideration curves of various cycle lengths. Similarly, 2 sheep in the constant light were seen to have a significant pattern in MHp. These same 2 sheep were subsequently found to have a significant pattern of extended duration utilizing the periodic analysis. Polynomial analysis also revealed that the initial curve (maximum to minimum) in MHp for groups B and C were of reduced duration (Figure II.2), relating to the reduced exposure time to an increasing or decreasing daylengths, respectively, as both these groups had been previously held at 12L:12D (Figure II.2 and II.3). The periodic analysis, confirmed the influence of light, as it showed that only the sheep exposed to a 52 week seasonal light pattern had a significant 52 week pattern in MHp.

Explanations for the influence of photoperiod on the circannual rhythm in MHp may be postulated from the results of group A. This group provides evidence for the existence of an endogenous rhythm in MHp, similar to that seen for estrual activity of seasonally breeding ewes. It has been shown that reproductive cycles of ewes become irregular, asynchronous and out of phase with the natural reproductive cycle under conditions which physically or functionally, removes the animal from the stimulus of photoperiodic cues (Karsch and Wayne, 1988). As with the extended estrous cycles observed for ewes maintained in a constant light regime (Kennaway et al., 1983), the metabolic cycles of ewes in group A were of extended duration and out of phase when compared to the ewes exposed to natural seasonal light. Maximal heat production values for group A occurred near the natural shortest day in contrast to that of all the groups in a seasonal light pattern, displaying maximal values approximately 15 weeks following the week of the shortest day. Thus, as for estrual activity, photoperiod serves to entrain the precise timing of the metabolic heat production rhythm, and may also modulate its amplitude.

The precise time of occurrence of peaks and nadirs in metabolic heat production for the ewes in seasonal light, did not occur exactly in accordance with the longest and shortest daylength periods. Blaxter and Boyne (1982), after analyzing data from domestic sheep, found that maximum heat production occurred in midsummer and minimum heat production in midwinter coinciding more precisely with maximum and minimum daylengths, respectively. In a recent study Baldock et al. (1988), observed that the heart rate of domestic sheep varied seasonally, with minimum values in December and maximum values in June. Assuming heart rate to be a reasonable indicator of energy metabolism of a resting or moderately exercised animal, minimum and maximum values again coincide with minimum and maximum daylengths, respectively. Studies involving wild ungulate species, have found variations in time of maximal and minimal heat production values. Generally, peak values have been observed in spring and summer but in some cases autumn, and lowest values in winter (Silver et al., 1969; Nilssen et al., 1984; Regelin et al., 1985; Renecker and Hudson, 1986).

Variations in the timing of peaks and nadirs in MHp can be explained in part by the functional implications of this cycle. This MHp rhythm serves as an adaptive mechanism in temperate and polar environments where food quantity and quality varies seasonally. Natural patterns in voluntary food intake for sheep, involves maximums during spring and summer and minimums during winter (Gordon, 1964). A photoperiod manipulated cycle in voluntary food intake has been experimentally shown in sheep and deer, which coincides with the metabolic rhythm (Simpson et al., 1983). In the above studies involving wild ungulates, food was provided *ad libitum* and a similar cycle in food intake to that observed for MHp was evident. The heat production associated with ingestion and digestion would be expected to vary seasonally as a result of variations in food intake. Therefore, peaks and troughs in MHp could be expected to occur at periods of maximal and minimal food intakes, respectively. The earlier onset of peaks and nadirs in MHp in the present study may therefore, have been a consequence of restricted food intake. This concept is examined in more detail in Chapter V.

Because of the known effects of food intake on MHp, studies have attributed food intake as the driving force responsible for seasonal MHp (Nilssen et al., 1984). Blaxter and Boyne (1982) however concluded from their analysis that a seasonal rhythm in metabolic rate was independent of feed intake and postulated that there was an additional seasonal component (possibly photoperiod) of metabolic rate. From the results of the present study, it may be suggested that metabolic rate is the physiological parameter photoperiodically driven and that appetite patterns may occur in response to metabolic changes. Increases in food intake may in turn, act in a feedback manner to modulate the phase of the MHp rhythms and accentuate the magnitude of the metabolic response.

The amplitude of the MHp response observed for ewes in a seasonal light pattern of ± 11% of the mean MHp value compares closely to the variation of ± 14% of the mean MHp reported for restrict fed Suffolk cross sheep (Blaxter and Boyne, 1982) and Soay rams (Argo and Smith, 1983). As mentioned before, food intake influences MHp and the degree of variation may be altered by feed restriction. Argo and Smith (1983) reported greater amplitudes in the heat production cycles of rams fed to appetite. Similarly, for wild ungulates fed *ad libitum*, greater degrees of seasonal variation in MHp were reported with differences of 40% (Regelin et al., 1985) and 120% (Renecker and Hudson, 1986) for moose, 50% for White-tailed deer (Silver et al., 1969) and 20% for Roe deer (Weiner, 1977). As conditions of measurement vary between the above studies the degree of seasonal variation in the heat production cycle may have been further influenced by additional variables, including ambient temperature, animal activity, and reproductive status, all of which were controlled in the present study.

The degree to which other intrinsic and extrinsic parameters influence the cycles in MHp is an area requiring further examination. Future studies examining the effects of controlled combinations of environmental parameters such as photoperiod and ambient temperature, may provide further insight into the timing and degree of the seasonal responses observed in MHp. Furthermore, reduction or alteration in the MHp response observed may be a consequence of domestication. Provision of shelter and food in winter reduces the selective pressure that would maintain seasonality in some physiological parameters. With domestication there has been deliberate selection for annual production of offspring, meat and wool, and seasonality in many physiological traits has been nearly eliminated in some lowland breeds of sheep (Kay, 1985).

Physiological explanations, to account for changes in measured resting MHp, based on the energy flow through the animal (Figure II.4), may be occurring in some of the individual components contributing to total Hp. The lack of treatment differences in food digestibility indicate that variations in MHp were not be accounted for by shifts in diet availability.

Furthermore, energy retention, as estimated by live weight and wool growth changes, did not strongly parallel the pattern of MHp or light pattern. Changes in body energy stores would in theory, be expected to occur, if energy expenditure increased while energy intake remained constant. If changes in body energy reserves are reflected in body weight changes, it would be expected that a decrease in weight, or because all ewes increased in weight throughout the study, a reduction in weight gain would occur during periods of increased metabolic heat production. This was generally not evident during the present trial with the exception of groups C and D which exhibited greater weight gain during the final 20 weeks, although coincident with the time of increasing MHp. Changes in live weight of a low magnitude may have occurred but not detectable by the measurement procedure. These more subtle fluctuations in weight may have contributed to the lower body weight of groups B, C and D at the end of the trial, suggesting that under constant light, the diminished or eliminated metabolic cycles of group A contributed to a more stable live weight gain and greater wool growth. Furthermore, shifts in body composition and therefore energy stores, may have occurred without changes in body weight. Forbes (1982) reported that when nutritional effects were removed by pair-feeding, lambs maintained in long daylengths (16L:8D) had longer leaner carcasses than lambs in short daylengths (8L:16D), with no apparent effect on carcass weight. This is an area requiring further research to provide insight into the underlying physiological changes relating to shifts in MHp and body energy reserves.

The Suffolk breed of sheep utilized in the present study, has retained its seasonality in terms of photoperiodically entrained rhythm in MHp. The presence of a innate rhythm in metabolic heat production was evident in some of the ewes maintained in a constant 12L:12D environment. Seasonal photoperiod, both artificial and natural, served to regulate the precise timing of the changes in metabolic heat production, with natural photoperiod accentuating this response. The implications of the existence of a cycle in metabolic rate for production situations may suggest alterations in the maintenance energy requirements of sheep associated with particular times of the year. However this is dependent on the production situation and may also vary with the breed of sheep, as variations have been shown in the degree of seasonality of voluntary food intake of different breeds of sheep (Manecton, 1989). Further research is required in order to provide understanding of interactive environmental variables, such as photoperiod, temperature and food intake and also the contribution of breed differences and animal behaviour patterns on seasonal cycles in energy metabolism.

Table II.1. Least square means (± SEM) of dry matter digestibility, live weights, weight gain and wool growth, and the maximum and minimum MHp values determined from polynomial regression analysis (quintic equation), for ewes exposed to four photoperiodic regimens.

	Group A	Group B	Group C	Group D
Dry matter digestibility (%)				
	$76.1^{a} \pm 0.3$	$75.4^{a} \pm 0.3$	$76.4^{a} \pm 0.3$	$75.2^{a} \pm 0.4$
Post shearing live weight (kg)				
Initial	$50.5^{a} \pm 1.6$	$50.2^{a} \pm 1.6$	$46.0^{ab} \pm 2.0$	$41.6^{b} \pm 1.8$
Final	$64.5^{a} \pm 1.3$	$59.4^{b} \pm 1.3$	$59.9^{b} \pm 1.5$	$57.7^{b} \pm 1.4$
Weight gain (kg/week)				
week 14 to 25				
	$0.43^{a} \pm 0.05$	$0.42^{a} \pm 0.05$	$0.45^{a} \pm 0.05$	$0.30^{a} \pm 0.05$
week 48 to 60				
	$0.17^{a} \pm 0.04$	$0.06^{a} \pm 0.04$	$0.06^{a} \pm 0.04$	$0.17^{a} \pm 0.04$
week 74 to 88				
	$0.004^{ab} \pm 0.04$	$-0.08^{a} \pm 0.04$	$0.05^{bc} \pm 0.04$	$0.14^{c} \pm 0.04$
Wool growth (g/week)				
	$77.1^{a} \pm 0.9$	$62.3^{bc} \pm 0.9$	$69.0^{ab} \pm 1.0$	$56.0^{c} \pm 0.9$
Maximum MHp				
Watts (W)	$76.3^{a} \pm 2.2$	$78.8^{a} \pm 2.0$	$76.2^{a} \pm 2.4$	$78.4^{a} \pm 2.2$
$W/kg^{.75}$	$3.47^{a} \pm 0.1$	$3.67^{a} \pm 0.1$	$3.77^{a} \pm 0.1$	$4.18^{b} \pm 0.1$
Week of maximum MHp				
(W)	$84.3^{a} \pm 1.5$	$71.0^{b} \pm 1.5$	$44.8^{c} \pm 1.8$	$44.2^{c} \pm 1.6$
$(W/kg^{.75})$	$84.8^{a} \pm 2.0$	$70.2^{b} \pm 1.8$	$40.5^{c} \pm 2.2$	$42.8^{c} \pm 2.0$
Minimum MHp				
(W)	$69.2^{a} \pm 1.5$	$63.3^{ab} \pm 1.5$	$64.3^{ab} \pm 1.9$	$63.7^{b} \pm 1.5$
$W/kg^{.75}$	$3.14^{a} \pm 0.1$	$3.07^{a} \pm 0.1$	$3.01^{a} \pm 0.1$	$3.16^{a} \pm 0.1$
Week of minimum MHp				
(Watts)	$55.7^{a} \pm 1.7$	$41.7^{b} \pm 1.7$	$72.8^{c} \pm 2.1$	$68.2^{c} \pm 1.9$
$(W/kg^{.75})$	$61.0^{a} \pm 1.8$	$41.0^{b} \pm 1.7$	$73.5^{c} \pm 2.1$	$69.8^{c} \pm 1.8$

$^{a\ b\ c}$ means with different superscript in a row differ ($P < 0.05$).

Group A, constant 12L:12D
Group B, sinusoidal pattern of artificial light, reverse of Group C.
Group C, sinusoidal pattern of artificial light, closely mimicking natural light (Group B and C, summer and winter 'solstices' 18L:6D and 6L:18D, respectively)
Group D, natural photoperiod (53.5° N latitude)

Table II.2 Polynomial analysis of the fifth degree (quintic equation) for MHp values (watts) for ewes in each photoperiodic regimen.

Group	Sheep no.	weeks from max to min MHp cycle 1	cycle 2	amplitude	R2	F value
A	48	30	27	7.5	0.03	1.108
	49	34	27	12.3	0.15	1.642
	74	40	26	9.4	0.13	1.528
	85	40	26	20.0	0.38	3.203 *
	239	31	26	14.2	0.13	1.518
	189	26	40	27.9	0.44	3.844 *
	mean	35	26	15.2		
B	20	23	30	24.1	0.52	4.926 *
	47	23	28	16.0	0.04	1.132
	81	23	25	14.9	0.64	7.528 **
	93	23	31	36.7	0.74	11.443 ***
	246	19	37	23.1	0.57	5.868 **
	39	23	25	32.5	0.63	7.228 **
	mean	22	29	24.5		
C	16	23	28	20.9	0.75	11.869 ***
	54	19	25	29.0	0.85	21.835 ***
	56	17	28	12.0	0.56	5.503 **
	107	28	31	20.8	0.57	5.756 **
	mean	22	28	20.7		
D	30	23	25	21.4	0.61	6.678 **
	31	22	28	17.6	0.25	2.211
	176	23	20	36.0	0.80	15.134 ***
	202	23	25	25.4	0.50	4.456 *
	64	22	22	31.8	0.73	10.858 ***
	mean	23	24	26.4		

* $0.01 < P < 0.05$ ** $0.001 < P < 0.01$ *** $P < 0.001$

Group A, constant 12L:12D
Group B, sinusoidal pattern of artificial light, reverse of Group C.
Group C, sinusoidal pattern of artificial light, closely mimicking natural light (Group B and C, summer and winter 'solstices' 18L:6D and 6L:18D, respectively)
Group D, natural photoperiod (53.5° N latitude)

Table II.3. Periodic regression analysis (cycle length=52 weeks) of resting MHp (watts) of Suffolk ewes exposed to one of four light regimens 20 observations/ewe for 71 weeks of the experiment.

Group	Sheep no.	Constant ± SEM	Phase angle (PA) wk of max MHp	Delay (MHp PA- light PA)	Amplitude (watts)	R^2	F value
A	48	72.3 ± 1.29	25.3	-26.4	7.8	0.21	2.29
	49	67.5 ± 1.02	34.8	-16.9	7.3	0.28	3.27
	74	74.4 ± 1.09	26.4	-25.3	6.6	0.21	2.31
	85	71.6 ± 1.63	23.1	-28.6	9.4	0.20	2.09
	239	72.3 ± 1.09	30.2	-21.5	9.0	0.34	4.33*
	189	82.2 ± 1.79	32.5	-19.2	6.3	0.09	0.80
	mean	73.4 ± 1.3	28.7	-22.9	7.7		
B	20	67.2 ± 1.11	15.7	-13.4	13.1	0.51	9.18**
	47	72.0 ± 1.40	19.8	-9.3	9.4	0.25	2.91
	81	71.5 ± 1.24	19.9	-9.2	10.6	0.35	4.67*
	93	77.4 ± 1.57	22.4	-6.7	19.9	0.54	10.26**
	246	67.3 ± 1.31	14.9	-14.2	12.4	0.46	5.96*
	39	73.8 ± 1.28	20.1	-9.0	16.8	0.57	11.07***
	mean	72.5 ± 1.4	19.3	-10.3	14.9		
C	16	71.0 ± 0.58	44.3	-11.4	11.5	0.75	25.36***
	54	72.9 ± 1.38	43.4	-12.3	13.5	0.43	6.30**
	56*	71.1 ± 0.94	47.4	-8.3	8.5	0.39	4.85*
	107	72.3 ± 1.19	42.4	-13.3	11.8	0.43	6.40**
	mean	71.8 ± 1.0	44.4	-11.3	11.3		
D	30	70.6 ± 1.22	44.4	-7.3	20.2	0.71	19.41***
	31	74.4 ± 1.16	48.2	-3.5	9.2	0.35	4.35*
	176	74.6 ± 2.43	40.5	-11.2	21.9	0.42	5.68*
	202	69.4 ± 1.46	37.0	-14.7	20.2	0.61	12.75***
	64	70.9 ± 1.68	43.2	-8.5	15.7	0.44	6.26**
	mean	72.0 ± 1.6	42.7	-9.0	17.5		

*n=18 observations.

* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$

Group A, constant 12L:12D

Group B, sinusoidal pattern of artificial light, reverse of Group C.

Group C, sinusoidal pattern of artificial light, closely mimicking natural light (Group B and C, summer and winter solstices' 18L:6D and 6L:18D, respectively)

Group D, natural photoperiod (53.5° N latitude)

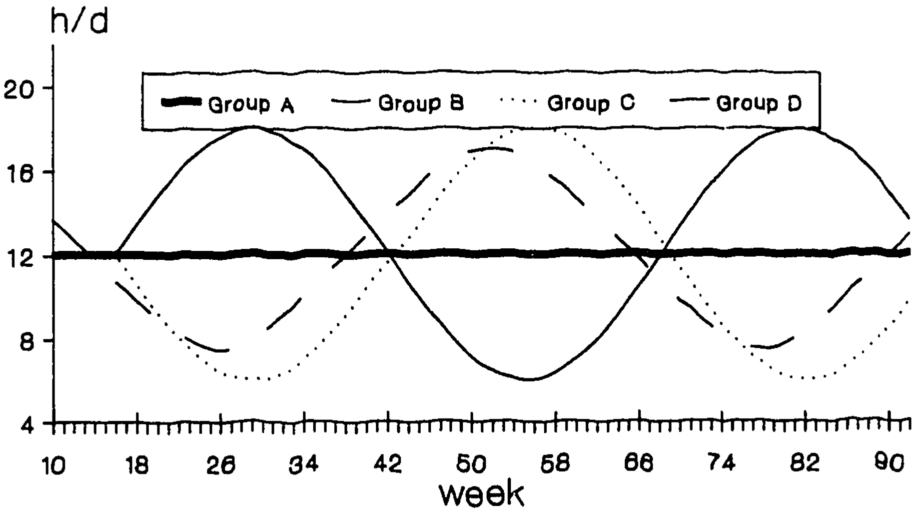
Table II.4. Periodic regression analysis (cycle length=52 weeks) of resting MHp (watts) of Suffolk ewes exposed to one of four light regimens, 15 observations/ewe for the final 52 weeks of the experiment

Group	Sheep no.	Constant ± SEM	Phase angle week of peak MHp	Delay (PA MHp- PA lights)	Amplitude (watts)	R^2	F value
A	48	71.4 ± 1.4	27.9	-23.8	6.6	0.18	1.30
	49	67.0 ± 1.3	36.0	-15.7	7.6	0.27	2.20
	74	74.1 ± 1.2	27.8	-23.9	5.3	0.17	1.25
	85	71.1 ± 1.7	27.2	-24.5	12.4	0.36	3.32
	239	72.3 ± 1.4	30.1	-21.6	8.6	0.28	2.34
	189	81.5 ± 2.0	32.0	-19.7	11.8	0.27	2.17
	mean	72.9 ± 1.5	30.2	-21.5	8.7		
B	20	67.7 ± 1.2	16.9	-12.3	12.1	0.55	7.25**
	47	72.3 ± 1.7	20.7	-8.5	10.0	0.26	2.09
	81	70.8 ± 1.0	14.9	-14.2	7.0	0.34	3.10
	93	79.6 ± 1.6	21.7	-7.4	24.2	0.70	14.18***
	246	67.1 ± 1.4	17.5	-11.6	9.5	0.38	3.63*
	39	74.9 ± 1.3	9.4	-9.7	18.7	0.70	14.26***
	mean	72.0 ± 1.4	18.5	-10.6	13.6		
C	16	70.6 ± 0.7	43.9	-11.8	13.0	0.81	24.90***
	54	71.7 ± 1.0	41.6	-14.1	18.4	0.81	25.06***
	56	70.5 ± 0.9	45.1	-10.6	8.7	0.49	5.80*
	107	72.0 ± 1.3	44.2	-11.5	14.4	0.56	7.64**
	mean	71.2 ± 1.0	43.7	-12.0	13.6		
D	30	70.3 ± 1.4	43.8	-7.9	21.7	0.74	17.07***
	31	73.5 ± 1.2	48.0	-3.7	11.9	0.50	6.05*
	176	76.6 ± 2.4	37.4	-14.3	21.7	0.47	5.33*
	202	70.0 ± 1.7	36.0	-15.7	20.2	0.60	8.83**
	64	71.5 ± 1.7	40.8	-10.9	16.2	0.51	6.28*
	mean	72.4 ± 1.7	41.2	-10.5	18.3		

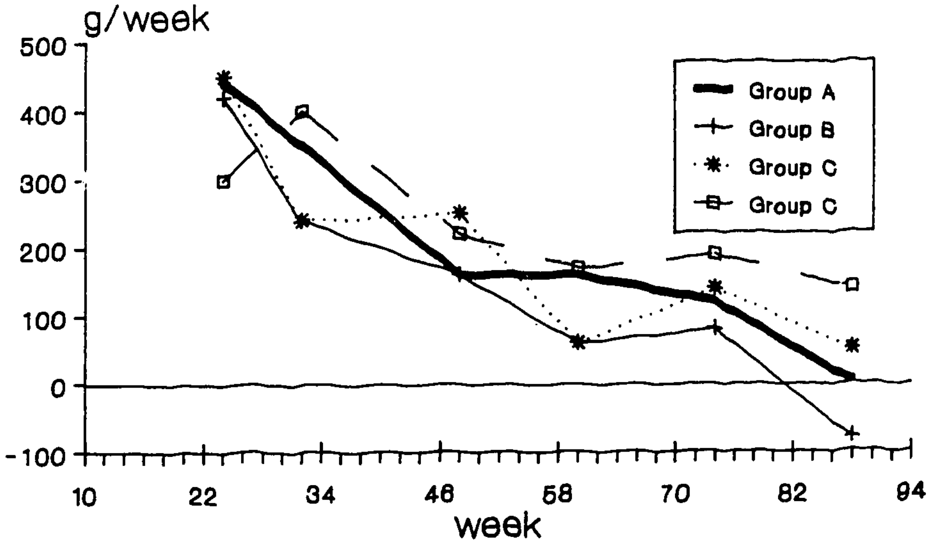
* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$

Group A, constant 12L:12D
Group B, sinusoidal pattern of artificial light, reverse of Group C.
Group C, sinusoidal pattern of artificial light, closely mimicking natural light (Group B and C, summer and winter 'solstices' 18L:6D and 6L:18D, respectively)
Group D, natural photoperiod (53.5° N latitude)

Figure II.1 Photoperiod regimens and the average weekly weight gain of each group

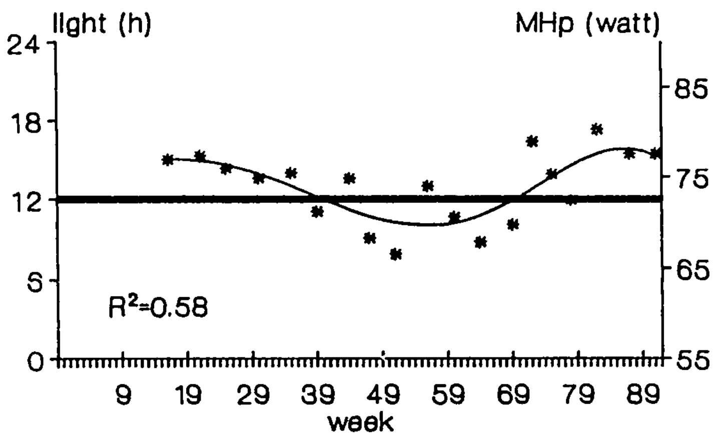


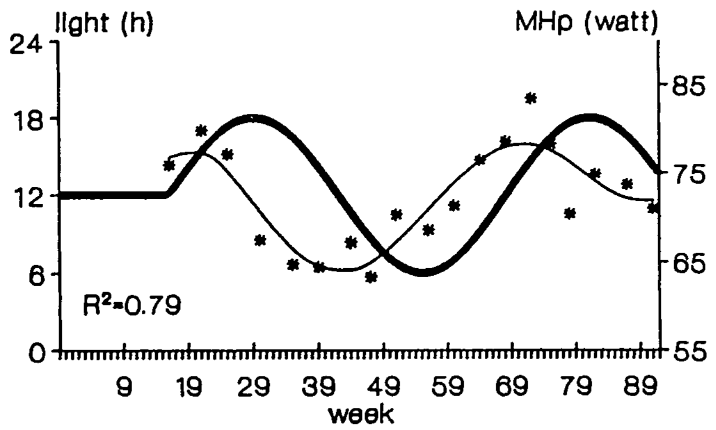
A. Light patterns

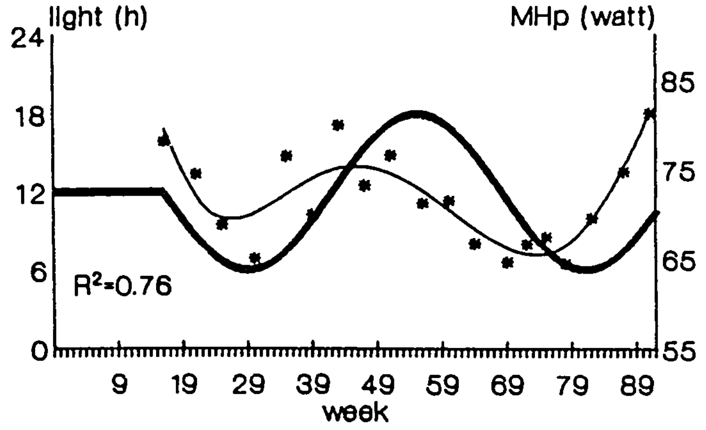


B. Weight gain

Figure II.2 Group mean resting metabolic heat production values for each photoperiodic regimen with the fitted polynomial function, quintic equation (wide line represents light pattern, * represents observed MHp, narrow line represents fitted MHp)


Group A (constant 12L:12D)


Group B (artificial light pattern)


Group C (artificial light pattern)

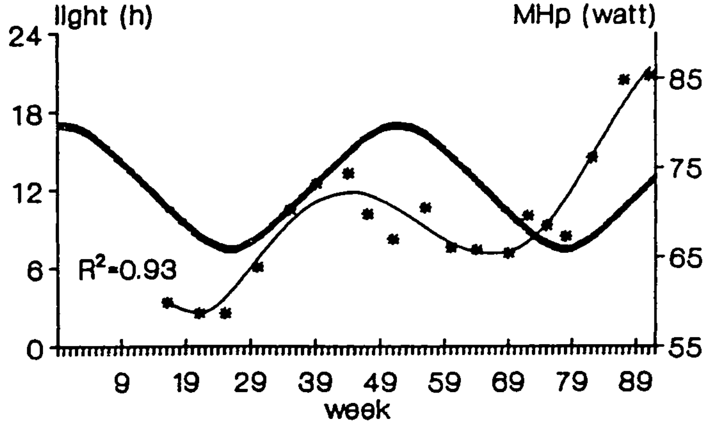
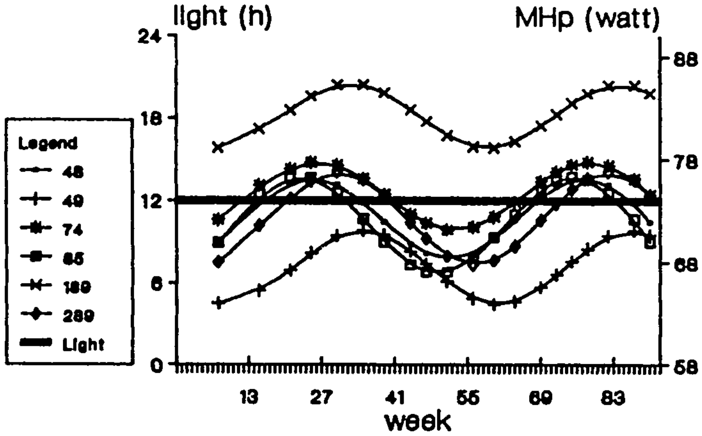
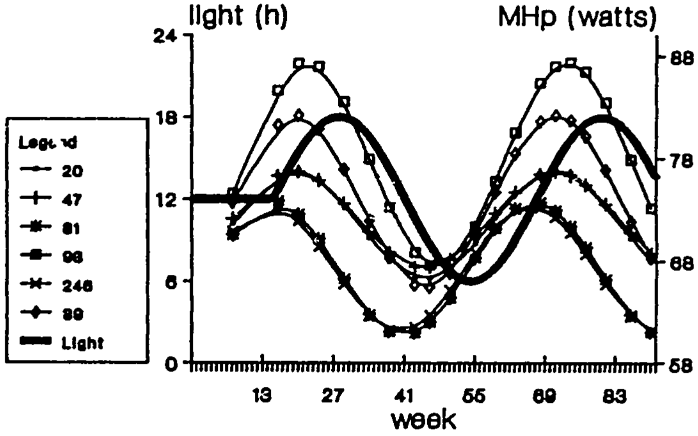

Group D (natural photoperiod)

Figure II.3 Predicted resting metabolic heat production patterns of ewes in each photoperiod regimen, as estimated utilizing periodic regression analysis (wide line represents light pattern, narrow line with symbol represents fitted MHp for each sheep)

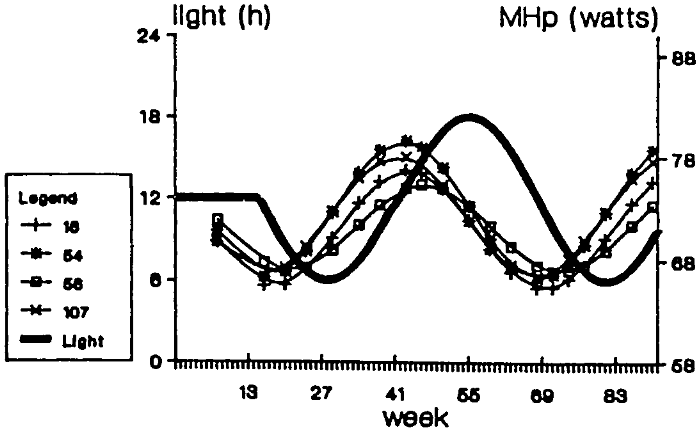
Group A (constant 12L:12D)



Group B (artificial light pattern)



Group C (artificial light pattern)



Group D (natural photoperiod)

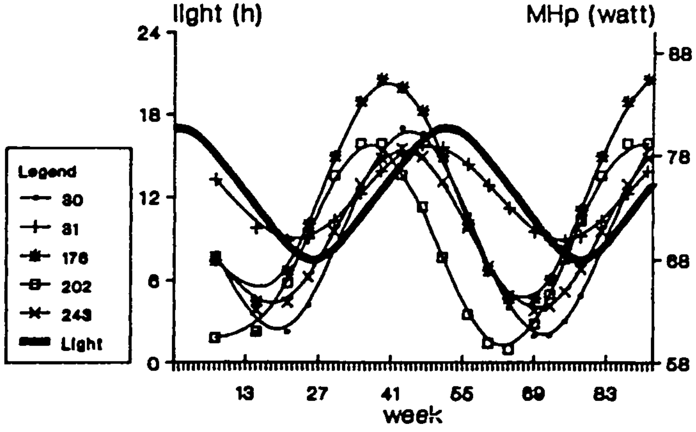


Figure II.4. Energy flow through an animal (from Ferrell, 1988)

Figure 11.4 has been removed due to the unavailability of copyright permission.

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III. INFLUENCE OF PHOTOPERIOD ON SEASONAL THYROID HORMONE CHANGES

INTRODUCTION

Prominent seasonal cycles in reproduction (Sadlier, 1969) and energy metabolism (Silver et al., 1969; Blaxter and Boyne, 1982; Regelin et al., 1985; Renecker and Hudson, 1986) occur in some wild and domestic species of ungulates originating in polar and temperate regions of the world. The physiological mechanisms governing these metabolic changes have not been fully elucidated, although distinct annual variations in the levels of various hormones have been implicated. Examples of hormones which have been found to vary seasonally in certain wild and domestic ungulates include, thyroid hormones (Ryg and Langvatn, 1982; Loudon et al., 1989), growth hormone (Ryg, 1982), and prolactin (Munro et al., 1980; Bubenik et al., 1983).

Thyroid hormones are known to regulate energy metabolism (Van Hardeveld, 1986) by increasing the rates of reactions in most cells of the body (Guyton, 1986). Thyroid hormones stimulate the rate of energy expenditure during rest and activity with reported maximal stimulation of basal metabolic rate (BMR) in humans and rats of 100-150% above normal BMR (Van Hardeveld, 1986). A number of environmental factors, including temperature (Galton, 1978), nutrition (Danforth et al., 1981) and emotional stress (Gregerman and Davis, 1978), have been shown to influence thyroid activity.

In sheep, changes in photoperiod influence the secretion of most of the anterior pituitary hormones including luteinizing hormone (Webster and Haresign, 1983), follicle stimulating hormone (Langford et al., 1987), thyroid stimulating hormone, prolactin and growth hormone (Munro, et al., 1980; Lincoln et al, 1980; Langford et al., 1987). Seasonal rhythms have been reported for thyroxine (tT4) and triiodothyronine (tT3) for white-tailed deer (Bahnak et al, 1981; Brown et al., 1983; Watkins et al., 1983), reindeer (Ryg and Jacobsen, 1982; Nilssen et al., 1984), red deer (Ryg and Langvtan, 1982; Loudon et al., 1989), and domestic sheep (Wallace, 1979). However in many studies involving wild ungulates there have been conflicting results, with reports of no seasonal change in tT4, but one for tT3 (Bubenik and Leatherland, 1984) or the reverse situation (Watkins et al., 1983).

It has been shown (Chapter II) that seasonal changes in photoperiod directly influenced the metabolic heat production of ewes, when known contributing factors of food intake, physical activity and ambient temperature were maintained near constant. If changes in thyroid activity contribute to the changes in metabolic rate, one would expect that the plasma hormone concentrations vary throughout the year, parallel to the metabolism changes.

The aim of the present study was to examine the influence of photoperiod on total and free (unbound) thyroxine and triiodothyronine concentrations in plasma and to examine their relationship to seasonal photoperiodic induced changes in metabolic heat production.

MATERIAL AND METHODS

Animals, Housing and Management

The detailed experimental procedure of animals, their housing and management are described in Chapter II; only a brief description is therefore presented here. Twenty-four Suffolk ewes born in February and March, were kept outdoors at 53.5°N latitude until they were 4 to 7 months of age. They were then brought indoors in June (18 ewes, groups A, B and C) or September (6 ewes, group D).

Experimental Design

The 18 ewes (groups A, B and C) were kept in light-proof rooms and exposed to an artificial light pattern of 12 h light, 12 h dark daily (12L:12D) for first 18 weeks. They were then assigned randomly to one of three artificial light treatments for a period of 76 weeks. The light environments were as follows: Group A, continued 12L:12D; Group B, a sinusoidal pattern of light change with initial increase in daily light; Group C, the reverse sinusoidal pattern of Group B, closely mimicking natural seasonal light, see solid lines in Figure III.1A to Figure III.1D. The artificial summer and winter 'solstices' were 18L:6D and 6L:18D, respectively. The lights were on automatic timers and adjusted weekly.

An additional group of six ewes (Group D) were brought into the experiment from outdoors, 4 weeks prior to the start of the artificial light treatments. This group was maintained in a windowed room and continued to be exposed to the natural light pattern for 53.5° N latitude. Accordingly, light intensity varied daily depending on season and prevailing weather conditions. All other conditions were the same as the other three groups.

Experimental Measurements

The methodology related to the metabolic heat production measurements has been described elsewhere (chapter I). Individual blood samples were collected once weekly, between 09:30 and 10:30 throughout the experiment via jugular venipuncture. Sampling began 4 weeks prior to imposing the light treatments. Immediately following collection, plasma was separated by centrifugation and stored at -20°C until assayed by radioimmunoassay, for total and free, thyroxine (tT4 and fT4) and triiodothyronine (tT3 and fT3) concentrations. During week 55 of the trial, when group B was in minimal light, and groups C and D in maximal light, the ewes were chronically cannulated 24 h prior to sampling and blood samples were collected at 30 minute intervals for a period of 25 h. A single dim red light (below detection limit of light meter, < 35 lux) aided blood sample collection in the dark period.

Hormone Assays

Plasma total and free T4 and T3 concentrations were measured using a solid-phase radioimmunoassay system, supplied in kit form (Diagnostic Products Corporation, CA, U.S.A.). The values for sensitivity and intra- and interassay coefficients of variation for each radioimmunoassay are shown in Table III.1. It was found that for the fT3 analysis some of the samples were below the limit of detection of the assay. For these samples the lowest detectable amount (0.05 pg/ml) was assigned as the value to the sample.

Statistical Analyses

To each set of thyroid hormone data for each ewe and for the treatment group averages, the following equation for a periodic curve was fitted:

$$Y = a_0 + a_1 \cos C X + b_1 \sin C X$$

where X was the observed time (weeks), expressed as units from the start of the experimental treatments, and C was a constant equal to 360° divided by a predetermined cycle length (the number of weeks in the light cycle=52) (Little and Hills, 1978). More detail on this analysis has been provided in Chapter II.

The week of maximum thyroid hormone concentrations was calculated (termed the phase angle, PA) and this was compared to both the week of peak light (PA of light) and the week of peak MHp (PA of MHp). The phase angle of MHp values was determined previously by periodic regression analysis and was described in detail in Chapter II. The difference between the phase angles of these parameters was referred to as the phase delay. A negative phase delay indicated that maximum thyroid concentrations occurred following maximum MHp and a positive phase delay indicated the reverse. Amplitude of the curve was also calculated (described in Chapter II) as the difference between minimum and maximum thyroid levels.

Analysis of variance (ANOVA) using the General Linear Model (GLM) procedure (SAS, 1988) was used to compare the computed means, amplitudes and phase delays for each treatment. The significance of mean differences were determined using a t-test equivalent to Fisher's least significant-difference test. Values are given as means ± standard deviation unless otherwise specified. ANOVA using the GLM procedure (SAS, 1988), was used to compare the hormone concentrations during the daylight, darkness and feeding periods from the 25 h sampling. Again the significance of mean differences were determined using a t-test equivalent to Fisher's least significant-difference test. Significance was assessed at $P<0.05$ unless stated otherwise.

RESULTS

One ewe from group A was replaced early in the trial, 14 weeks prior to the start of the light treatments. Three sheep, two from group C and one from group D, were removed during the course of the experiment for reasons unrelated to the experimental treatments and were not replaced. Data from these ewes were not used in the statistical analysis.

Circadian patterns

An example of a circadian profile of hormone concentrations as determined from the 25 h sampling trial, is shown in Figure III.2. Daily variations were greatest for tT3. Total T3 and T4 were significantly elevated during and for 4 hours following feeding. No significant differences were observed in relation to daylight or darkness periods for tT3 and tT4 concentrations with average values shown in Table III.2. Similarly, there were no significant differences between daylight, darkness and feeding concentrations for fT3 and fT4. Therefore the sampling period of 16 to 17 h postprandial (0900 to 1000) was considered to provide a reliable estimate of thyroid concentrations and changes therein, when sampling was limited once weekly.

Circannual patterns (Periodic regression analyses)

Table III.3 summarizes the level of significance of the periodic regression analysis for tT3, tT4, fT3 and fT4, based on a fitted 52 week cycle. For the groups exposed to a seasonal light pattern, a significant sinusoidal pattern was evident for 14 of 15 ewes for tT3, and 12 of 15 ewes for fT3 and fT4. This pattern was generally highly significant (P<0.01) for group B. Only 2 of 6 ewes in constant light, had a significant 52 week sinusoidal pattern for tT3, fT3 and fT4. The results for tT4 were less convincing with only 8 of 15 regressions being significant for the ewes in seasonal light and none of the regressions were significant for the ewes in constant light. This sinusoidal pattern was found to be reversed for the groups exposed to a reverse seasonal light pattern (Figure III.1A-D).

The overall average tT3 concentration, given as the constant term calculated using the equation of Little and Hills', was significantly higher for the group in natural light (group D) in comparison to groups in artificial light (groups A, B and C) (Table III.4). Average fT3 concentrations for Group D were also significantly higher than the two groups in seasonal artificial light (groups B and C). This corresponds to average MHp per $kg^{.75}$ which was found to be significantly greater for group D in comparison to groups A, B and C. No significant treatment differences were observed in the average concentrations of tT4 or fT4.

The time of the occurrence of predicted maximum thyroid hormone levels, in relation to weeks of exposure to an increasing daylength, (for the sheep having a significant sinusoidal pattern), are shown in Table III.4 (phase delay). Group B, exposed to the artificial light pattern in reverse of natural light, displayed peak values in tT3, fT3 and fT4 after a longer exposure time to an increasing daylength, than the other groups. This was found to be significantly longer in comparison to group D, in natural light (8.5 ± 2.3 weeks), with peak values for group B occurring following 50% longer exposure time to increasing daylength (16.4 ± 1.5 weeks). When the timing for thyroid hormone peaks for the ewes in group A (only ewes exhibiting a significant sinusoidal pattern), was compared to the natural light pattern, maximum values were found to occur approximately 5 weeks following (tT3) or approximately 10 weeks preceding (fT3 and fT4) the week of the natural shortest day.

When amplitude (expressed as ± percentage of the mean thyroid hormone concentration) was calculated (Table III.4), group B was found to have a significantly greater amplitude for fT3 and fT4 than the other groups. Total T3 and T4 did not differ in amplitude between the groups exposed to seasonal light.

Relationship between maximum MHp and maximum thyroid hormone concentrations (phase delay) was calculated as the difference between the week of predicted maximum MHp and the week of maximum tT3, tT4, fT3 and fT4 concentrations of each group (Table III.4). Generally, the predicted thyroid hormone curves paralleled the predicted MHp curves (Figure III.1A-D). Significant differences in this relationship for groups exposed to a seasonal light pattern, were observed for tT3 and fT3. Peak values in tT3 preceded peak MHp by approximately 4 to 5 weeks for groups C and D, whereas the reverse situation was evident for tT3 for group B (-4.0 weeks), in the reverse light situation. Similarly for fT3, peak values preceded peak MHp values by 5.0 and 2.0 weeks for group C and D, respectively. However peak fT3 corresponded closely with peak MHp for group B (0.1 ± 1.3). Groups C and D generally had maximum thyroid concentrations prior to maximum MHp values (2.9 ± 2.6 weeks). The time of predicted peak levels in thyroid hormones for the ewes in constant light did not coincide as closely to the times of peaks in MHp.

DISCUSSION

The overall mean concentrations of tT3, tT4, and fT4 (Table III.4) were similar to those obtained from sheep in previous studies (Sutherland and Irvine, 1974; Guerrini and Bertchinger, 1983; Millar and Albyt, 1985). The overall mean value for fT3 in the present study of 2.3 ± .11 pmol/l was lower than the value for ewes obtained by Millar and Albyt (1985), of 6.3 ± 0.3 pmol/l. Differences in analytical methods may account for this variation in fT3 concentrations.

The circadian pattern observed in the present study demonstrates the immediate influence of ingestion of a meal on thyroid hormones as was evident by elevated levels at and following feeding time. Lincoln et al (1982) examined hourly fluctuations of tT3 and tT4 in rams subjected to short (8L:16D) or long (16L:8D) days and reported a consistent diurnal fluctuation for tT3 with low values coincident with the end of the dark period. A similar variation in relation to light was not evident from present 24 h samples, but tT3 was more variant than tT4. However our circadian analysis was conducted on only one sheep from reverse artificial light treatments for bihourly samples. Lincoln et al (1982) found noticeable hour to hour variation in tT3 values which was assumed to be due to episodic secretion. This may not have been detected presently from the selected samples analyzed. A more extensive analysis could help determine the presence or absence of possible episodic secretion in tT3.

The significant sinusoidal pattern for tT3, fT3 and fT4 for the majority of ewes exposed to a seasonal light pattern occurred in a similar manner in response to the light changes. The ewes in reverse seasonal light provide support for photoperiodic control as they displayed a reverse sinusoidal pattern in thyroid changes. Maximal concentrations of thyroid hormones were always observed while the ewes were exposed to an increasing daylength and the time of occurrence was therefore determined in relation to the weeks exposed to increasing daylength. However, it was evident that thyroid levels began increasing prior to the shortest day (Figure III.1A-D) and may therefore suggest that the response is to shortening daylength. Similarly, induction of reproductive activity occurs in shortening daylength.

The significant sinusoidal pattern seen for 1 or 2 ewes in constant light for tT3, fT3 and fT4 is suggestive of the presence of an innate rhythm. This pattern was out of phase with the natural light group indicating that photoperiod changes serve to regulate the precise time of occurrence of these hormonal changes.

The longer response time for peak concentrations of tT3, fT3 and fT4 to occur, following the nadir in light, in group B, may be due to the fact that they were exposed to the complete opposite light pattern than previously experienced, and therefore required longer exposure in order to elicit a response. This group also displayed a larger amplitude in the response of free T3 and T4, indicating that the reverse artificial light pattern to what would naturally be experienced served to induce a more profound response.

Of the thyroid hormones examined, tT3 and fT3 were consistently the best indicators of response to daylength changes. Total T4 was found to be the least responsive as indicated by fewer ewes having a significant sinusoidal pattern. T4 is the prohormone which is broken down to the metabolically active form, T3 (Nunez, 1988). A host of pathways influence the levels of thyroid hormones in the plasma, including the secretion rate of T4 and T3 by the thyroid, the conversion of T4 to T3 outside the thyroid, the metabolic clearance of T3 and the exchange of T4 and T3 between plasma and the tissues (Visser, 1988). From the results, the greater responsiveness of T3 and the fact that it is considered the active form of the hormone, suggests that these plasma levels are a closer indicator of the changes in energy metabolism (MHp).

One of the main functions of thyroid hormones is in the control of metabolic rate by regulating cellular oxidation processes (Millar and Albyt, 1985). It is therefore expected that the time of peak thyroid concentrations should coincide closely with the time of maximum MHp, as evidenced in the data. This supports the notion that the influence of photoperiod on MHp is mediated by means of thyroid activity. The advanced peak in tT3 concentrations in relation to peak MHp for groups C and D may be due to shifts in the metabolism of thyroid hormones, whereby there is an increased uptake and utilization by tissues during peak time of MHp which is not reflected by plasma hormone levels. Thyroid hormone activity has been shown to be determined predominantly by intracellular concentrations of fT3 in the tissues (Visser, 1988). The coincidence of exact time of peak levels of T3 with MHp for group B, may be a consequence of an exaggerated response by this group, therefore excess in hormone levels.

The time of occurrence of peak and trough thyroid levels, in relation to the natural seasons, would coincide generally with spring and fall, respectively, in terms of the photoperiodic environment. This is in agreement with the seasonal pattern of thyroxine reported by Wallace (1979) for domestic sheep, fed a constant maintenance diet. Maximum tT4 plasma concentrations were evident in the spring and minimums in fall (Wallace, 1979).

The seasonal change in thyroid levels of wild ungulates has been closely associated with the seasonal change observed in voluntary food intake (Ryg and Jacobsen, 1982; Chao and Brown, 1984; Loudon et al., 1989). Seal et al. (1978) found that tT3 levels of fawns in autumn was strongly correlated with their energy intake. Ryg and Jacobsen (1982) similarly found that tT3 levels of reindeer were positively correlated with food intake and changes in tT3 levels could be induced by altering food intake. In most studies where thyroid function has been examined in wild ungulates, feed was provided *ad libitum*, therefore feed related changes in thyroid cannot be removed from thyroid changes related to other factors.

It is clear from the present results that changes in daylength directly influence the seasonal cycle in thyroid levels irrespective of food intake. Previous evidence of photoperiodic influence on thyroid function was demonstrated for restrict fed sheep exposed to 16 week block periods of long (16L:8D) and short (8L:16D) days (Lincoln et al., 1980). Increased circulating concentrations of tT3 and tT4 occurred during each period of long days (Lincoln et al, 1980).

The functional significance of increasing thyroid levels with increasing photoperiod would be to increase basal metabolic rate (as estimated by changes in MHp) which then stimulates appetite and increases food intake, coinciding with times when food quality and quantity is similarly increasing. Gordon (1964) found that domestic sheep had maximum food intake during summer months. This increased food intake would serve in a feedback manner to increase both thyroid levels (as evidenced by increased T3 at and following feeding) and MHp, and therefore shift the time of maximum values and amplitude of the response. Ryg (1982) postulated that changes in tT4 could stimulate food intake which could in turn cause increased levels of tT3 as much of tT3 is derived from peripheral deiodination of tT4. However in the present study increases in tT3 generally preceded tT4. As mentioned this may reflect changes occurring in the utilization of tT4 (ie. decrease in breakdown of tT4 to tT3 resulting in increased plasma levels of tT4 following peaks in tT3).

Plasma levels of thyroid hormones are only one parameter which may be utilized to describe seasonal thyroid function. Possibly a more direct measure of changes in thyroid function could be determined from studies examining photoperiodic influences on the secretion and clearance rate of these hormones as well as possible changes in the receptor sites for these particular hormones. Other areas of interest with regard to photoperiodic influences on physiological functions may include the examination of higher levels of control, ie. thyroid stimulating hormone (TSH) from anterior pituitary, and thyrotropin releasing hormone (TRH).

The present results indicate that seasonal photoperiod serves to entrain the seasonal pattern observed in thyroid levels which likely serves to stimulate the changes in metabolic response. This was supported by the use of a reverse seasonal light pattern to the natural pattern which elicits a reverse pattern in thyroid levels and MHp. These changes in physiological parameters of the animal could also be responsible for the seasonal changes that have been observed in voluntary food intake of animals.

TABLE III.1. Performance characteristics for each radioimmunoassay

	Sensitivity	Intra-assay CV (%)	Inter-assay CV (%)
Total T3	0.11 nmol/l	5.5	6.5
Total T4	3.90 nmol/l	5.3	7.3
Free T3	0.31 nmol/l	6.0	7.5
Free T4	0.13 nmol/l	7.2	8.3

T3 - triiodothyronine, T4 - thyroxine

TABLE III.2. Average circadian thyroid hormone concentrations (mean ± SEM).

	Feeding	Daylight	Darkness
Total T3 (ng/ml)	$0.86^{a} \pm 0.07$	$0.56^{b} \pm 0.05$	$0.56^{b} \pm 0.05$
Total T4 (ug/ml)	$0.042^{a} \pm 0.002$	$0.037^{b} \pm 0.001$	$0.037^{b} \pm 0.001$
Free T3 (pg/ml)	$0.83^{a} \pm 0.10$	$0.72^{a} \pm 0.07$	$0.59^{a} \pm 0.07$
Free T4 (ng/dl)	$0.70^{a} \pm 0.03$	$0.63^{a} \pm 0.02$	$0.63^{a} \pm 0.02$

[a,b] means with a different superscript in a row differ ($P<0.05$).

TABLE III.3 - Summary of F values and level of significance for periodic regression analysis for the various thyroid hormones

Group	Sheep	tT3 (n=37)	tT4 (n=37)	fT3 (n=26)	fT4 (n=26)
A	48	1.69	0.19	2.91	3.00
	49	5.68*	0.20	2.03	4.31*
	74	0.57	0.08	4.04*	1.19
	85	3.44*	2.28	5.41*	4.39*
	189	1.39	1.20	1.52	1.46
	239	0.87	1.15	3.20	2.49
B	20	11.83***	11.25***	20.58***	24.72***
	47	6.21**	0.98	10.36***	5.35*
	81	5.22*	3.95*	3.41*	17.51***
	93	7.71**	1.42	20.41***	18.37***
	246	14.16***	10.39***	20.70***	44.18***
	39	7.69**	2.00	25.85***	11.46***
C	16	23.85***	10.77***	4.64*	9.88***
	54	3.31*	3.32*	6.86**	1.08
	56	7.07**	6.60**	4.32*	5.86**
	107	7.88**	2.95	1.70	1.75
D	30	17.47***	19.56***	10.66***	4.99*
	31	9.98***	1.53	2.72	4.39*
	176	14.81***	10.89***	5.56**	5.12*
	202	4.54*	0.39	1.44	2.35
	64	2.14	1.06	3.98*	4.05*

* $P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$

Group A; constant 12L:12D
Group B; artificial sinusoidal pattern of light change, the reverse of natural light
Group C; artificial sinusoidal pattern of light change, reverse of Group B, closely mimicking natural light
(artificial summer and winter 'solstices' for Groups B and C were 18L:6D and 6L:18D, respectively)
Group D; natural photoperiod (53.5° N latitude)

TABLE III.4. Summary of hormone concentrations, phase delay of peak concentrations of thyroid hormones in relation to light, amplitude, and phase delay of thyroid concentrations in relation to MHp as determined utilizing periodic regression analysis outlined by Little and Hills (1978).

	Group A*	Group B	Group C	Group D
A. Average concentrations				
tT3 (ng/ml)	0.91^{ab} ± 0.033	0.82^{a} ± 0.033	0.94^{b} ± 0.040	1.08^{c} ± 0.036
tT4 (ug/ml)	0.06^{a} ± 0.003	0.06^{a} ± 0.003	0.06^{a} ± 0.004	0.07^{a} ± 0.003
fT3 (pg/ml)	1.45^{ab} ± 0.064	1.36^{b} ± 0.064	1.36^{b} ± 0.078	1.61^{a} ± 0.070
fT4 (ng/dl)	0.85^{a} ± 0.043	0.83^{a} ± 0.043	0.80^{a} ± 0.053	0.85^{a} ± 0.047
(B. Phase delay in relation to light (weeks of exposure to increasing daylength).				
tT3	4.9^{a} ± 1.6	19.4^{b} ± 0.9	9.2^{ac} ± 1.3	10.4^{c} ± 2.3
tT4	+ +	15.1^{a} ± 3.7	12.7^{a} ± 3.7	16.3^{a} ± 4.5
fT3	-9.6^{a} ± 3.3	15.3^{b} ± 1.9	8.7^{bc} ± 2.7	7.4^{c} ± 2.7
fT4	4.1^{a} ± 2.8	14.5^{b} ± 1.6	9.8^{bc} ± 2.8	7.7^{c} ± 2.0
C. Amplitude (± % of the mean thyroid hormone concentration)				
tT3	18.7^{a} ± 0.04	30.6^{b} ± 0.02	30.2^{b} ± 0.03	24.1^{ab} ± 0.03
tT4	+ +	25.1^{a} ± 0.03	26.2^{a} ± 0.03	22.4^{a} ± 0.03
fT3	34.8^{a} ± 0.10	67.1^{b} ± 0.06	36.9^{ac} ± 0.09	51.5^{ac} ± 0.10
fT4	18.9^{a} ± 0.05	33.7^{b} ± 0.03	21.9^{abc} ±0.05	17.7^{ac} ± 0.03
D. Phase delay in relation to MHp (weeks)				
tT3	-2.0^{a} ± 1.9	-4.0^{a} ± 2.0	4.7^{b} ± 2.4	4.7^{b} ± 2.4
tT4	-7.6^{a} ± 2.6	-3.5^{a} ± 3.7	1.2^{a} ± 3.7	-2.4^{a} ± 3.7
fT3	11.7^{a} ± 1.3	0.1^{b} ± 1.3	5.1^{c} ± 1.8	2.0^{bc} ± 2.9
fT4	8.2^{a} ± 1.5	0.9^{b} ± 1.5	5.1^{ab} ± 2.1	2.9^{ab} ± 2.1

Values given are least square means ± standard error of mean

* time of maximum calculated in relation to natural light pattern

^{a,b,c} means with different superscript in a row differ ($P < 0.05$).

\+ no significant periodic response

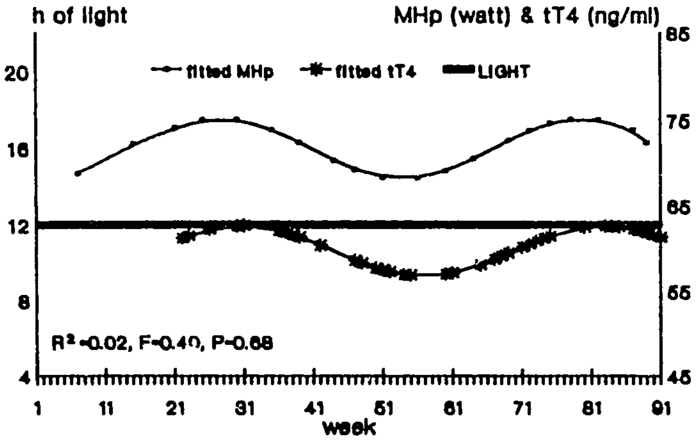
Group A; constant 12L:12D.

Group B; artificial sinusoidal pattern of light in reverse of natural light.

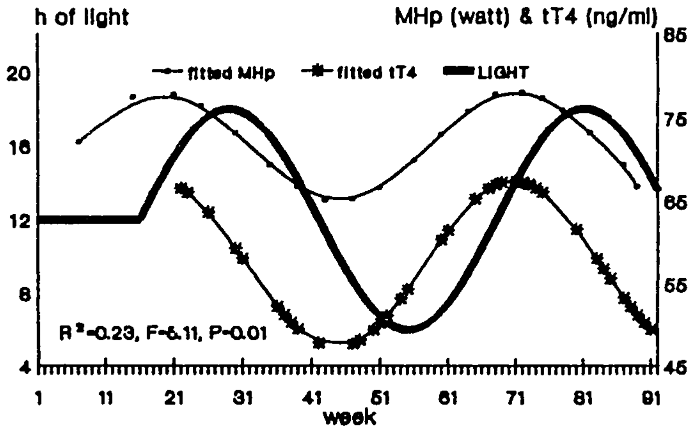
Group C; artificial sinusoidal pattern, closely mimicking natural light (artificial summer and winter 'solstices', 18L:6D and 6L:18D, respectively).

Group D; natural photoperiod, 53.5° N latitude.

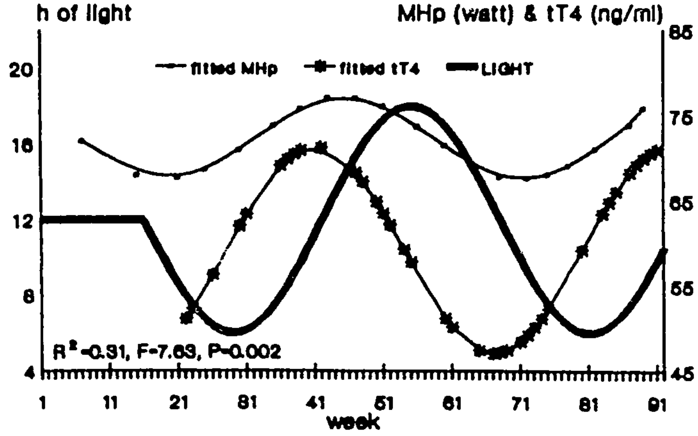
Figure III.1A. Fitted curves for group means for plasma total T4 concentrations and metabolic heat production values determined utilizing periodic regression analysis (R^2, F value and level of significance given for the tT4 regression analysis).



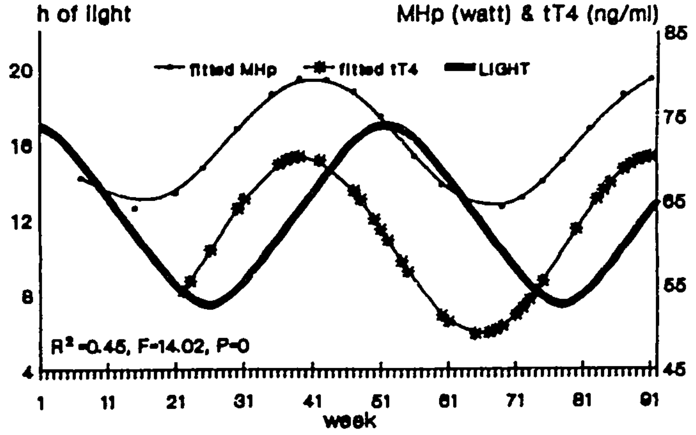
Group A (constant 12L:12D)



Group B (artificial light)



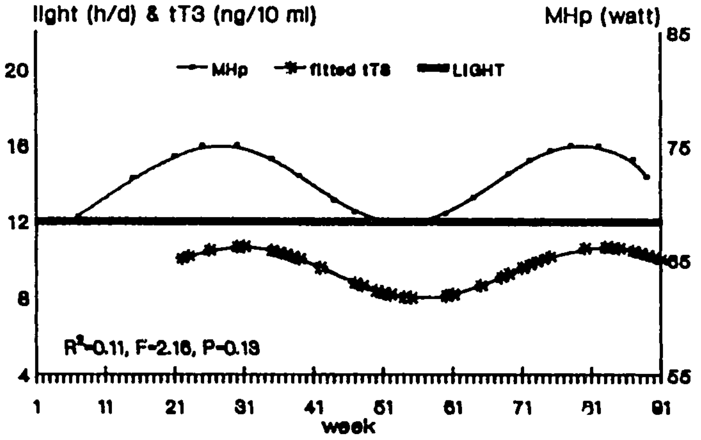
Group C (artificial light)



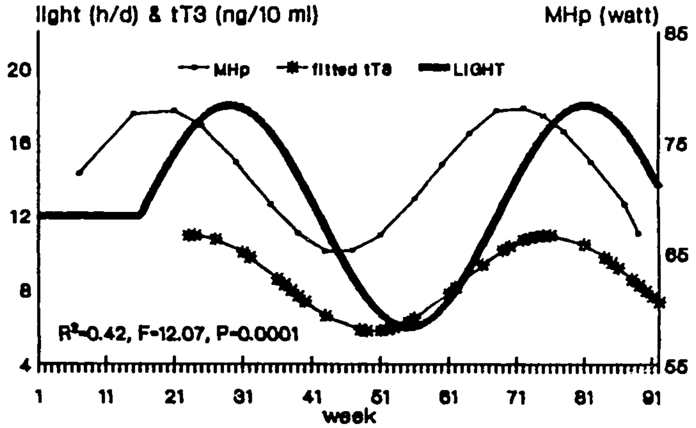
Group D (natural light)

Figure III.1B. Fitted curves for group means of plasma total T3 concentrations and metabolic heat production values determined utilizing periodic regression analysis (R^2, F value and level of significance given for the tT3 regression analysis).

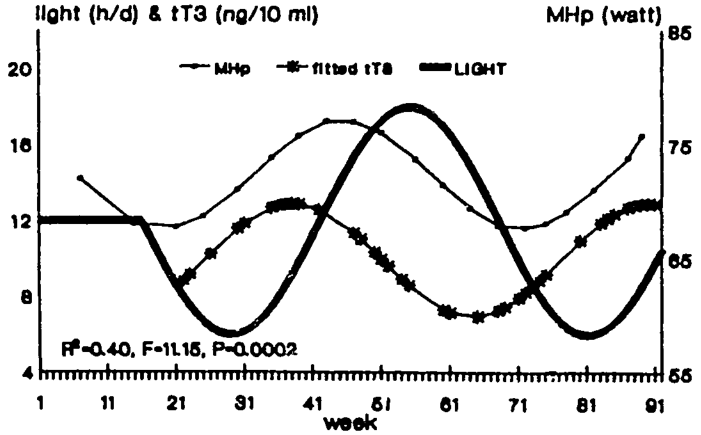
Group A (constant 12L:12D)



Group B (artificial light)



Group C (artificial light)



Group D (natural light)

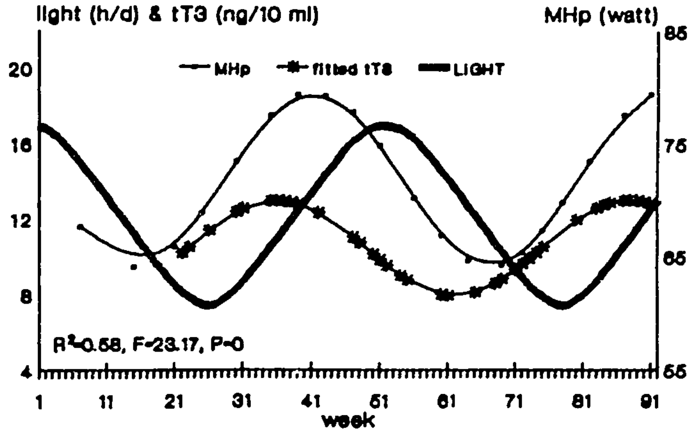
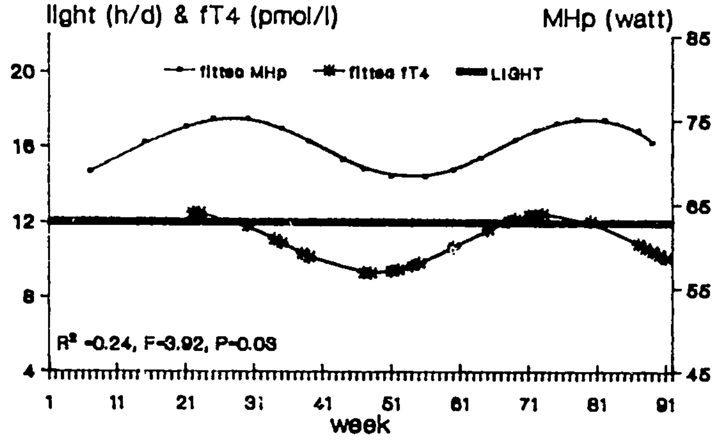
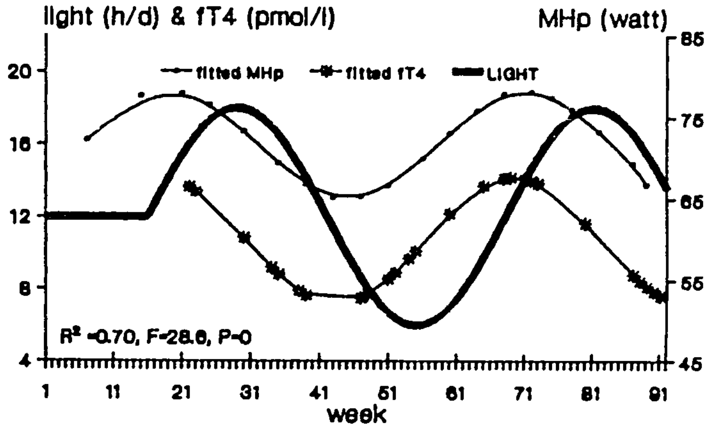


Figure III.1C. Fitted curves for group means of plasma free T4 concentrations and metabolic heat production values determined utilizing periodic regression analysis (R^2, F value and level of significance given for fT4 regression analysis).

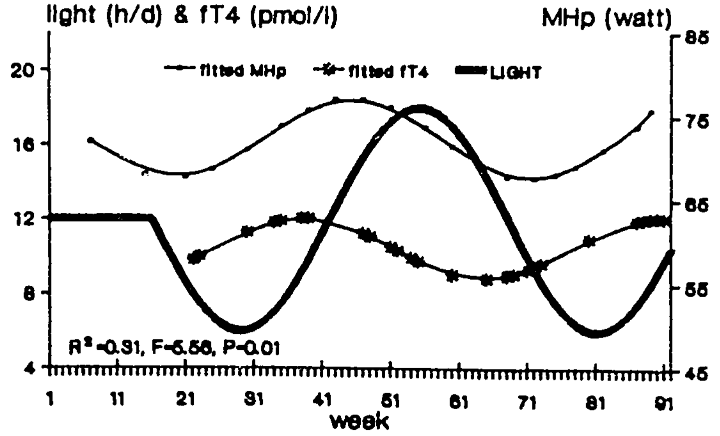
Group A (constant 12L:12D)



Group B (artificial light)



Group C (artificial light)



Group D (natural light)

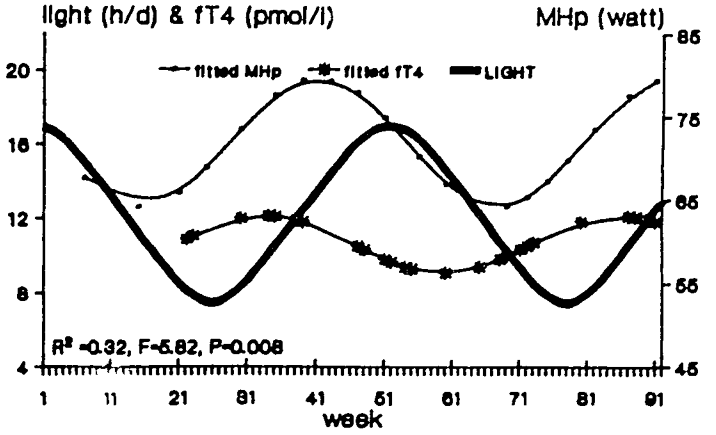
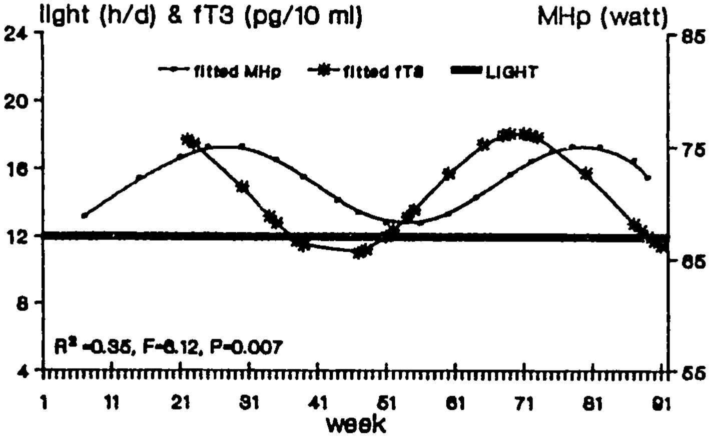
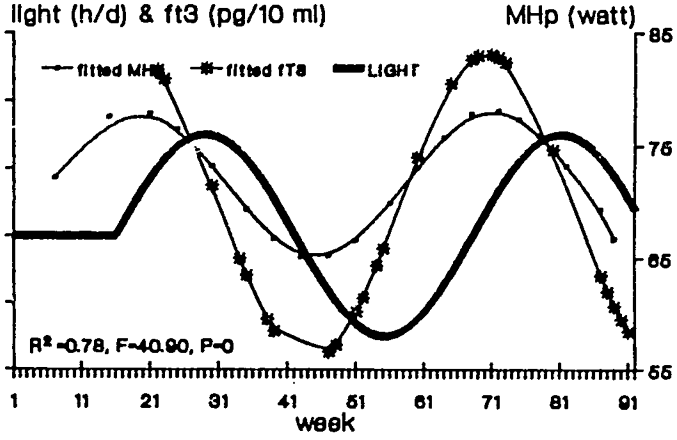


Figure III.1D. Fitted curves for group means of plasma free T3 concentrations and metabolic heat production values determined utilizing periodic regression analysis (R^2, F value and level of significance given for fT3 regression analysis).

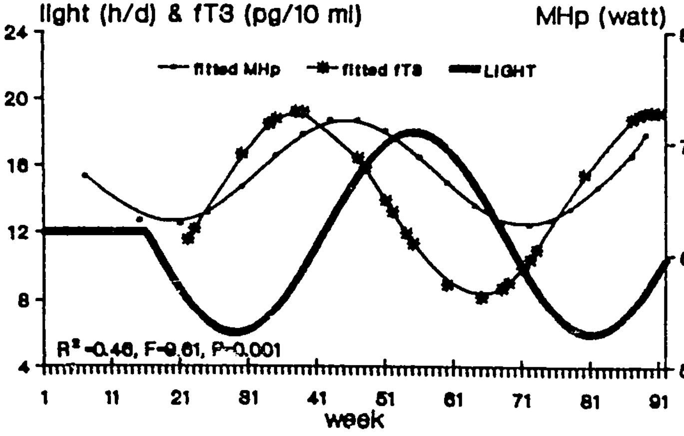
Group A (constant 12L:12D)



Group B (artificial light)



Group C (artificial light)



Group D (natural photoperiod)

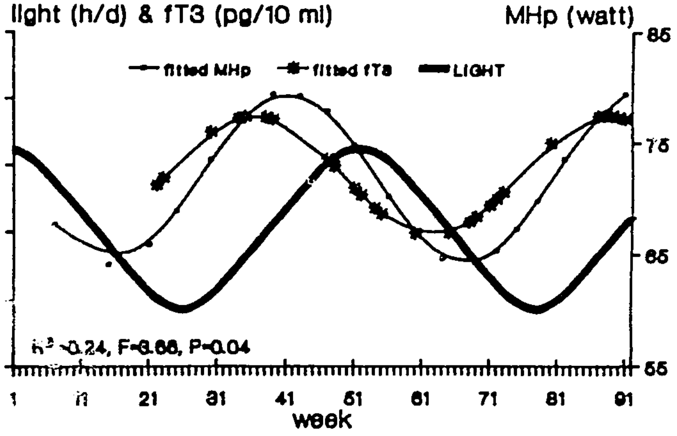
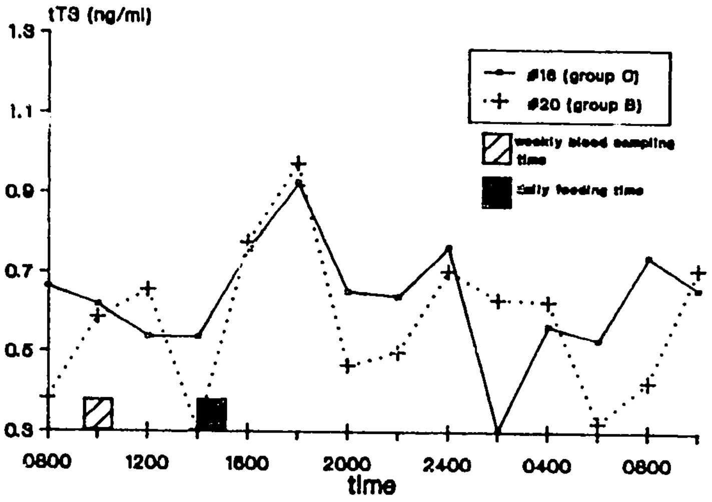
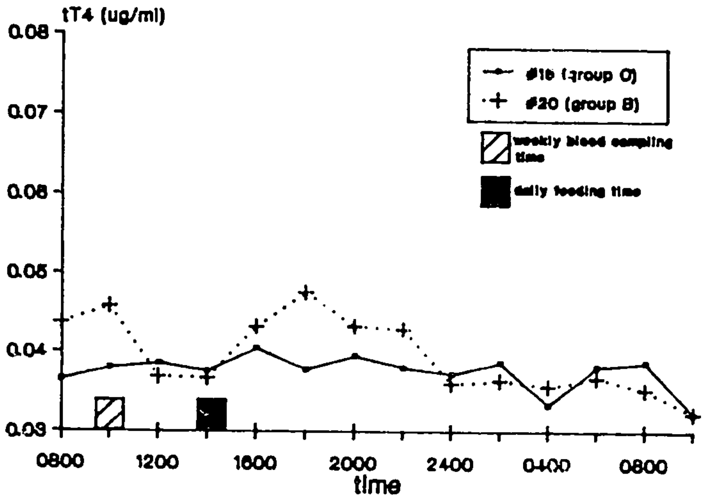
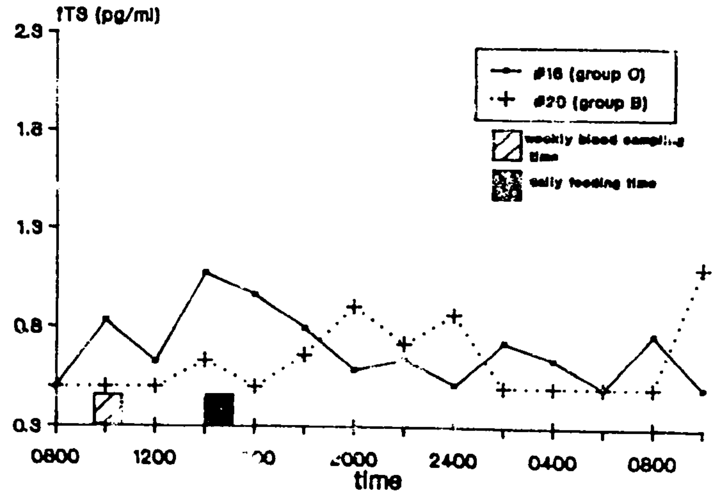
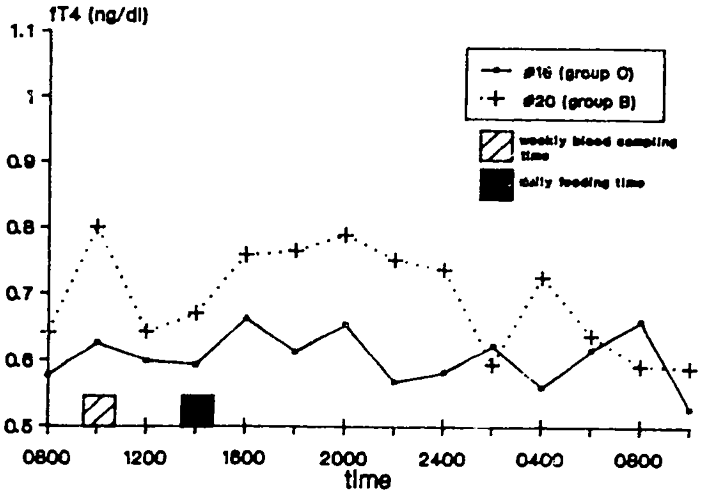


Figure III.2 Circadian profiles of plasma thyroid hormone concentrations


tT3 (ng/ml)
1.3
1.1
0.9
0.7
0.5
0.3
0800
1200
1600
2000
2400
0400
0800
time
#16 (group O)
#20 (group B)
weekly blood sampling time
daily feeding time


tT4 (ug/ml)
0.08
0.07
0.08
0.05
0.04
0.03
0800
1200
1600
2000
2400
0400
0800
time
#16 (group O)
#20 (group B)
weekly blood sampling time
daily feeding time


fT3 (pg/ml)
2.3
1.8
1.3
0.8
0.3
0800
1200
2000
2400
0400
0800
time
#16 (group O)
#20 (group B)
weekly blood sampling time
daily feeding time


fT4 (ng/dl)
1.1
1
0.9
0.8
0.7
0.6
0.5
0800
1200
1600
2000
2400
0400
0800
time
#16 (group O)
#20 (group B)
weekly blood sampling time
daily feeding time

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IV. INFLUENCE OF PHOTOPERIOD ON REPRODUCTIVE FUNCTION OF EWES AND RELATIONSHIP TO THYROID HORMONE CONCENTRATIONS

INTRODUCTION

Most domesticated breeds of sheep have distinct seasonal patterns in reproductive activity which are regulated by seasonal changes in daylength. Yeates (1949) demonstrated that the onset of estrous cyclicity in sheep occurred in response to decreasing photoperiod. Similarly, termination of estrous cyclicity resulted following exposure of ewes to an increasing photoperiod. Studies have shown that there is variation in the onset and termination of the breeding season mainly related to breed, age, and geographical location (Pelletier et al., 1986; Quirke and Hanrahan, 1985). Recent studies by Karsch and Wayne (1988) have suggested that although an endogenous rhythm is present in the ewe, photoperiodic changes serve to synchronize the onset and termination of the estrous period.

In the sheep, the hormones related to this reproductive phenology, including luteinizing hormone, follicle stimulating hormone and progesterone, have a distinct circannual pattern. One primary hormonal change linked with the regulation of estrous and anestrous periods has been in the negative feedback effects of oestradiol on tonic LH secretion (Haresign et al., 1985), with daylength being a major factor affecting changes in estrogen sensitivity (Kennaway et al., 1987). An increase in this negative feedback coincides with the period of seasonal anestrus and results in a low frequency of episodic LH secretion, below that required to promote the final phases of follicle development and maturation (Haresign et al., 1985). Prolactin also exhibits a circannual rhythm regulated by photoperiod, but its relationship to reproductive function remains unclear (Kennaway, et al., 1987). Recent evidence given by Nicholls et al. (1988), has also suggested that the thyroid gland plays a role in the seasonal reproductive response, serving in the regulation of the termination of estrous cyclicity.

The primary objective of the present study was to utilize the reproductive response of Suffolk ewes as an index of responsiveness to photoperiod changes as a part of a major study examining the photoperiodic effects on metabolic heat production (MHp), thyroid function and food intake. The present study allowed for the examination of the sensitivity of the onset and termination of the reproductive response to artificial and natural seasonal changes in photoperiod and to constant photoperiod (12L:12D) over a 76 week period. This was then compared with changes in plasma thyroid levels.

MATERIALS AND METHODS

Animals, Housing and Management

The detailed experimental procedure concerning animals, their housing and management has been described elsewhere (chapter II); only a brief description is therefore presented here. The study was conducted over a 94 week period (18 week preliminary, 76 weeks of photoperiodic treatments), of restricted feeding. It involved the use of 24 Suffolk ewes which were 5 to 7 months of age at the start of the trial. The ewes were caged individually in metabolism crates in one of four light regimens.

Experimental design

Initially 18 ewes were kept in light-proof rooms and exposed to an artificial light pattern of constant 12 h daily light (12L:12D) for 16 weeks. The ewes were then assigned randomly to one of three artificial light regimens for a period of 76 weeks. The light environments were as follows; group A, constant 12L:12D; group B, artificial sinusoidal pattern of light change in reverse to the natural light pattern, with an initial increase in daily light; group C, reverse artificial sinusoidal pattern to group B, which closely mimicked the natural seasonal light changes. The artificial summer and winter 'solstices' were 18L:6D and 6L:18D, respectively. The lights were set by automatic timers and adjusted weekly. Details of the type of artificial lighting utilized and the light intensity in the rooms are given in chapter II.

An additional group of six ewes (group D) were brought into the experiment in September and had previously been kept in a penned area outdoors. This group was maintained in a windowed room and exposed to the natural seasonal light pattern for Edmonton, Alberta, Canada, located at 53.5° N latitude. The light intensity for group D varied daily depending on climatic conditions. The light patterns for all groups are shown in Figure IV.1.

Experimental measures

Blood samples were collected from each ewe once weekly, between 09:30 and 10:30, via jugular venipuncture. Sampling began 4 weeks prior to the start of the artificial light changes. Plasma was immediately separated by centrifugation and stored at -20°C until assayed for progesterone (P4) and total and free thyroxine (tT3 and fT3) and triiodothyronine (tT4 and fT4).

Hormone assays

Plasma progesterone (P4) and total and free T3 and T4 concentrations were measured using a solid-phase radioimmunoassay system which was supplied in kit form (Diagnostic Products Corporation, CA, U.S.A.) The values for the sensitivity and intra- and interassay coefficients of variation for each radio-immunoassay are shown in Table IV.1.

Estrous cycle length of the ewe is 16-17 days with progesterone levels elevated between days 4-14 of the cycle (Goodman, 1988), hence weekly samples should detect most times of estrous (elevated P4 levels), with an occasional week missed. Generally progesterone concentrations greater than 1 ng/ml are utilized to indicate of ovarian activity (Poulton and Robinson, 1987). The first and final plasma progesterone concentrations equal to or greater than 2 ng/ml were considered as times of initiation and termination of estrous activity. Estrous cyclicity was considered to be consecutive weeks of plasma progesterone concentrations greater than 1 ng/ml with no more than 3 consecutive weeks of concentrations less than 1 ng/ml.

Statistical analyses

The progesterone profiles were used to determine the timing of estrous and anestrous periods in each ewe. One way analysis of variance (ANOVA) using the General Linear Models (GLM) procedure (SAS, 1988), was used to compare the onset and termination of the reproductive activity of the three groups in seasonal light. Periodic regression analysis was utilized to examine curvilinear relationships of total and free T3 and T4 concentrations to the light patterns imposed and this has been described in detail in chapter III. The timing of onset and cessation of estrous cycles was compared to the fitted sinusoidal patterns observed for total and free T3 and T4 concentrations. ANOVA (SAS, 1988) was also utilized to compare the concentrations of free T3 and T4 at the onset, middle and termination of estrous cycles. The significance of the mean differences were determined using a t-test equivalent to the Fisher's least significant-difference (LSD) test. Values are given as means ± standard deviation and significance was assessed at the $P<0.05$ level, unless otherwise specified.

RESULTS

Two ewes from group C and one ewe from group D were removed during the experiment for reasons unrelated to the experimental treatments imposed. Plasma samples collected from these animals up until their time of removal were utilized in the hormonal analysis. One ewe in group C showed no estrous activity at any time during the trial and was therefore excluded from the statistical analyses.

Circannual Progesterone (P4) patterns

Plasma progesterone concentrations during the period of estrous ranged from approximately 1 to 8 ng/ml. Figure IV.2, illustrates a typical progesterone profile utilized for the determination of the onset and cessation of estrous cycles. As shown in Table IV.2, the ewes in natural light (group D), compared to those in artificially changing light, required a significantly longer exposure time to decreasing photoperiod for the onset of first estrous cycles. However this was not found for onset of te second estrous cycles, with group [illegible] having initiation of estrous following the same exposure time to decreasing daylength as group C exposed to the similar artificial light pattern. No significant differences were observed for the time of termination of estrous cyclicity among groups. No significant differences were observed for the duration of estrous cycles between groups exposed to a seasonal light pattern, though group B appeared slightly longer (Table IV.2).

The ewes in constant 12L:12D (group A) did not display a set pattern of reproductive cycles, with some ewes exhibiting short irregular activity and some ewes having extended cycles. Initial plasma samples of one ewe in group A, (brought into the trial as a replacement in the fourth week of 12L:12D), indicated estrous cyclicity, which ceased 8 to 10 weeks earlier than the natural light group. This ewe similarly began and ceased the next estrous cycles at approximately the same time as the ewes in natural light. The other ewes in group A showing estrous cyclicity, began at week 39 to 43. They continued cycling for 34 to 44 weeks which was 50% greater than for those in seasonal light. These ewes were approximately 63 weeks of age, and had been exposed to 12L:12D for 45 weeks, when estrous activity began. Other ewes in Group A displayed periods of estrous activity, but not distinct cyclicity, beginning week 47.

The ewes in Group C and D were 43.8 ± 3.3 and 41.5 ± 8.4 weeks of age respectively when estrous cycling began. The ewes in Group B, in the reverse artificial light began estrous cyclicity at 60.0 ± 2.7 weeks of age. The ewes maintained in constant light (group A) showed signs of estrous activity or cyclicity at 68.8 ± 6.9 weeks of age.

Relationship of P4 patterns and thyroid patterns

When estrous activity was examined in relation to predicted thyroid hormone patterns, there was found to be a relationship such that the onset of estrous cycles coincided with the point of decreasing or lowest levels of thyroid hormones, and the cessation of estrous cycles coincided with the time of increasing or maximal thyroid hormone levels. The periods of estrous cyclicity are shown in relation to the predicted thyroid curves (as determined from periodic regression analysis, Chapter III), for each group, in relation the light patterns imposed (Figure

IV.1A-D).

The relationship between the cessation of estrous cycles and the thyroid concentrations (Table IV.3), was calculated as the week of maximum thyroid concentration minus the week of cessation of estrous cycles. Group B, had cessation of estrous cycles 10.0 ± 3.1 weeks prior to the peak in thyroid hormone concentrations, which was significantly different from the time for group C and D expose[illegible]everse light pattern. Groups C and D, had termination in estrous cycles close to the time of maximal thyroid levels, (2.6 ± 3.0 and 2.3 ± 5.9 weeks prior to maximal levels, respectively).

The termination of estrous cycles coincided most closely with fT3 and fT4 concentrations, suggesting that the plasma concentrations may be the factor of greater importance. Termination of estrous cycles resulted when plasma fT3 and fT4 were approximately 1.8 pg/ml and 1.0 ng/dl, respectively, for all the groups exposed to a seasonal light pattern, as estimated vis[illegible]m Figures IV.1C and IV.1D. Group B exhibited higher variat[illegible] fT3 and fT4, whereby cessation of estrous cycles occurred sooner in relation to maximal thyroid but was at the time when plasma fT3 and fT4 concentrations were already 1.8 pg/ml and 1.0 ng/dl, respectively. The average plasma concentrations of fT3 and fT4 at the onset, middle and termination of estrous cycles for each group are shown in Table IV.4. Concentrations at the onset and middle of estrous were significantly lower than those at the termination of estrous. The calculated average concentration of fT3 and fT4 at the termination of estrous was 1.88 ± 0.55 pg/ml and 1.04 ± 0.20 ng/dl, respectively (Table IV.4).

This close relationship was not as clear betwe [illegible] rmination of estrous and tT3 and tT4 concentrations. Group B in a reverse artificial light pattern to groups C and D, was found to have lower plasma concentrations of tT3 and tT4 at the termination of estrous cycles.

DISCUSSION

The artificial seasonal light regimens imposed proved to be effective in eliciting the typical reproductive response of seasonally breeding sheep, with cyclic estrous activity beginning when daylength was decreasing and ending when daylength was increasing (Yeates, [illegible]). As mentioned, certain hormonal changes have been implicated in the mechanism by which photoperiod elicits this response (Walton et al., 1977; Thimonier, 1981; Kennaway, 1987).

Present results are indicative of thyroid hormone involvement in the regulation of the timing of estrous cycles, as decreased and increased plasma levels of thyroid hormones were coincident with the initiation and termination of estrous cycles, respectively. Free T3 and T4 may have a greater influence, as similar plasma concentrations between groups were evident at the termination of estrous and these hormones were also found to be the most responsive to photoperiod changes. These findings are in support of recent studies, whereby thyroid was found to be involved in the proper termination of reproductive activity in sheep (Nicholls et al., 1988). Nicholls et al. (1988) found that thyroidectomizing ewes in the summer during anestrous had no influence on the onset of estrous cyclicity but did profoundly disrupt the onset of anestrous. All thyroidectomized ewes continued to cycle beyond the end of the normal breeding season and a number continued throughout the entire period of normal anestrous (Nicholls et al., 1988). Nicholls et al. (1988) reported that a single injection of 50 ug of thyroxine (tT4) permitted full reproductive shutdown in thyroidectomized birds which had been in a state of permanent sexual maturity for several years. Prolactin has been shown to have a similar circannual pattern to thyroid, with maximums in summer and minimums in winter and when this increase was delayed, a similar delay was observed for the onset of anestrous (Curlewis et al., 1988).

More extensive studies examining the relationship of thyroid changes and reproductive function are necessary in order to determine the causal link between these and the mechanism of how thyroid exerts this influence. Thyroid changes have previously been linked most closely with patterns in food intake (Ryg and Jacobsen, 1982; Chao and Brown, 1984; Ryg, 1984). Present findings have shown that thyroid increases and decreases were closely associated with increases and decreases in metabolism, respectively (chapters II and III). This has an adaptive significance in the natural environment situation, whereby increased thyroid activity and metabolism would stimulate food intake coinciding with the time of increased food availability. In relation to reproductive function this would enable the attainment of proper body condition, ensuring successful conception and gestation in the following reproductive cycle. It appears that the latent periods in the reproduction system, allows for the activation of other physiological systems, all of which are kept in tune with the environment through photoperiodic cues. Thyroid is likely one hormone, in conjunction with other hormones such as prolactin, that exerts an influence in an interactive manner on various physiological changes, including termination of reproductive function and onset of increases in energy metabolism.

Present findings support the current theory of the presence of an endogenous reproductive rhythm which is synchronized by light changes. The ewes held in continuous 12L:12D began to show periods of estrous activity and in some cases cyclicity, without any changes in photoperiod. However, the time of their estrous cycles was found to be out of phase with the natural reproductive cycle (group D). Although previous theories (Yeates, 1949), described the role of photoperiod as driving the reproductive cycles of seasonally breeding sheep, current evidence indicates that photoperiod serves as a synchronizer, thus ensuring an appropriate phasing between the seasonal reproductive cycle and environmental cues (Karsch and Wayne, 1988). In experiments which physically or functionally removes the animal from changes in the photoperiodic environment, reproductive activity has been shown to persist but is seen to become irregular, asynchronous and out of phase with the natural reproductive cycle (Karsch and Wayne, 1988).

The extended cycle duration of some ewes in group A is similar to findings of Howles et al. (1982), whereby rams exposed to constant long daylight (16h), from 4 to 38 months of age, had rhythmical changes in testis volume and prolactin concentration with periodicities of around 35 weeks. This rhythmical change was not likely due to 'remembered' pre-experience, as the animals received only 4 months of natural increasing photoperiod between birth and onset of treatment (Howles et al, 1982). Similarly, ewes in the present study had received only 4 to 5 months of natural increasing photoperiod from birth to the start of exposure to 12L:12D. The exception in Group A was the one ewe brought in as a replacement which had been previously exposed to the natural summer solstice and 3 weeks of natural decreasing photoperiod. A 12L:12D environment would be a sudden decrease in photoperiod and has been shown to induce the onset of reproductive cycling in sheep when initiated at summer solstice (Nicholls et al, 1989). The earlier cessation of this first estrous cycles for this ewe supports findings of Nicholls et al. (1989), whereby ewes exposed to constant 12L:12D beginning at the summer solstice had estrous cycles which ceased earlier by 1 to 2 months in comparison to ewes exposed at the summer solstice to constant 8L:16D or to the natural daylength changes.

The other ewes in group A which were held in constant light prior to the summer solstice, did not exhibit initiation of estrous activity at expected times. The previous photoperiodic history has been shown to be important for the entrainment of the endogenous reproductive rhythms. Spring born lambs held in constant long days equivalent to summer solstice starting at summer solstice do not get initiation of reproductive activity at the normal time whereas adult ewes maintained in constant long days from the summer solstice are able to begin reproductive activity at the appropriate time when they have previously experienced changes in photoperiod (Ebling and Foster, 1988).

In summary, the timing onset and termination of estrous cycles for all ewes exposed to seasonal light, as determined in relation to the light changes, was similar to the timing reported previously for Suffolk ewes, whereby breeding season began approximately 10.5 weeks following the summer solstice and ceased approximately 8 weeks following the winter solstice (Robinson and Karsch, 1988). The fact that group D took longer to respond to a decreasing daylength for onset of first estrous cycles, relates to other parameters required for the attainment of puberty. This includes not only the inductive influence of daylength changes, but also the age and more specifically the body condition of the ewes. The liveweight of group D at the initiation of estrous was 42.0 ± 3.0 kg. Generally, for Suffolk ewes to reach puberty, body weight must be 50% of their adult weight (Hafez, 1980). The adult weight of Suffolk ewes is generally from 75 to 90 kg, therefore group D began cycling at the anticipated time, in relation to body size requirements and the appropriate inductive photoperiod.

This study demonstrated the existence of an endogenous rhythm in reproductive function as evidence by group A and also provided evidence of thyroid involvement, through changes in thyroid hormone concentrations, in the cessation of estrous cycles in domestic sheep.

Table IV.1 Performance characteristics for each radioimmunoassay

	Sensitivity	Intra assay CV (%)	Inter assay CV (%)
tT3	0.11 nmol/l	5.5	6.5
tT4	3.90 nmol/l	5.3	7.3
fT3	0.31 pmol/l	6.0	7.5
fT4	0.13 pmol/l	7.2	8.3
P4	0.16 nmol/l	7.2	8.8

Table IV.2. Summary of the weeks of exposure to a decrease or increase in daylength for initiation or termination of estrous cycles, respectively, for the groups exposed to a seasonal light pattern[*].

Group	cycle	Onset of estrous cycles (weeks of ↓ light)	Termination of estrous cycles (weeks of ↑ light)	Duration of estrous (week)
B	1st	$10.0^{a} \pm 1.3$	$6.5^{a} \pm 1.0$	$21.2^{a} \pm 1.9$
	2nd	$10.3^{a} \pm 1.6$		
C	1st	$8.6^{a} \pm 1.4$	$8.8^{a} \pm 1.1$	$15.8^{a} \pm 2.1$
	2nd	$12.3^{a} \pm 1.6$	$8.7^{a} \pm 3.2$	$20.7^{a} \pm 3.4$*
D	1st	$17.3^{b} \pm 1.3$	$7.3^{a} \pm 1.0$	$16.3^{a} \pm 1.9$
	2nd	$12.2^{a} \pm 1.4$		

Values given are least square means ± standard error of the mean (SEM).

^{a,b} means with different superscript in a column differ ($P<0.05$).
* n=3 sheep

Group B, artificial sinusoidal pattern, the reverse of natural light
Group C, artificial sinusoidal pattern, mimicking natural light. (artificial summer and winter solstices, 18L:6D and 6L:18D, respectively.)
Group D, natural photoperiod, 53.5° N latitude

[*] Group A were exposed to constant 12L:12D, therefore initiation and termination of estrous in relation to light changes could not be evaluated and are therefore not included in the above table.

Table IV.3. Difference between predicted week of maximum thyroid concentrations (Phase angle, PA) and estimated week of termination of estrous cycles (TE).

Group	Sheep no.	tT3-TE	tT4-TE	fT3-TE	fT4-TE
A	48	13.2	27.3	7.9	8.8
	49*	-	-	-	-
	74*	-	-	-	-
	85	5.0	2.3	-5.9	-2.4
	189*	-	-	-	-
	239	4.2	-0.7	-20.4	-8.9
	mean	7.5	9.6	-6.1	-0.8
B	20	12.6	7.5	10.2	9.5
	47	10.8	14.1	5.5	6.9
	81	17.4	13.5	11.0	8.5
	93	13.0	9.3	10.3	7.5
	246	11.8	12.7	7.3	8.5
	39	12.5	3.3	9.2	7.6
	mean	13.0	10.1	8.9	8.1
C	16	4.8	8.1	3.9	6.8
	54*	-	-	-	-
	56	1.9	4.0	0.9	0.1
	107	0.1	2.0	0.6	-2.4
	mean	2.3	4.7	1.8	1.5
D	30	-0.5	2.6	1.4	-0.4
	31	0.2	0.1	-7.1	-3.9
	176	7.6	12.4	7.2	8.9
	202	7.1	10.6	3.6	1.1
	64	2.2	-6.7	-9.4	-4.2
	243	5.9	9.2	7.2	1.3
	mean	3.8	4.7	0.5	0.5

* ewes did not display estrous cycles

Group A, constant 12L:12D
Group B, artificial sinusoidal pattern, the reverse of natural light.
Group C, artificial sinusoidal pattern, closely mimicking natural light (artificial summer and winter solstices for Groups B and C were 18L:6D and 6L:18D, respectively)
Group D, natural photoperiod, 53.5° N latitude

Table IV.4. Average free T3 and T4 concentration at the onset, middle, and termination, of estrous cycles, for groups exposed to a each photoperiod regimen.

	Phase of Estrous		
	Onset	Middle	Termination
A. Free T3			
Group A	1.18^{a} ± 0.11	1.13^{a} ± 0.12	1.98^{a} ± 0.29
Group B	0.86^{b} ± 0.09	0.79^{b} ± 0.10	1.90^{a} ± 0.23
Group C	0.85^{ab} ± 0.13	1.03^{ab} ± 0.14	1.94^{a} ± 0.33
Group D	0.86^{b} ± 0.09	0.72^{b} ± 0.10	1.82^{a} ± 0.23
B. Free T4			
Group A	0.75^{ab} ± 0.08	0.73^{a} ± 0.09	1.21^{a} ± 0.10
Group B	0.75^{b} ± 0.06	0.67^{a} ± 0.07	1.04^{a} ± 0.08
Group C	0.68^{ab} ± 0.09	0.71^{a} ± 0.10	0.96^{a} ± 0.11
Group D	0.55^{a} ± 0.06	0.67^{a} ± 0.07	0.97^{a} ± 0.08

Values are given are least square means ± standard error of the mean (SEM).

[a,b] means with different superscript in a column differ ($P<0.05$).

* n=3 sheep

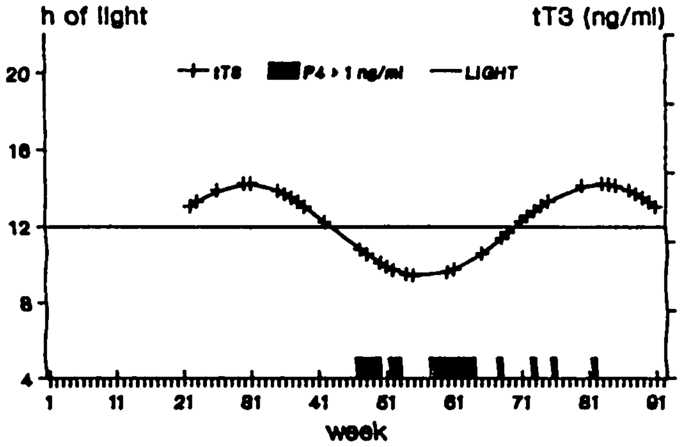
Group A, constant 12L:12D

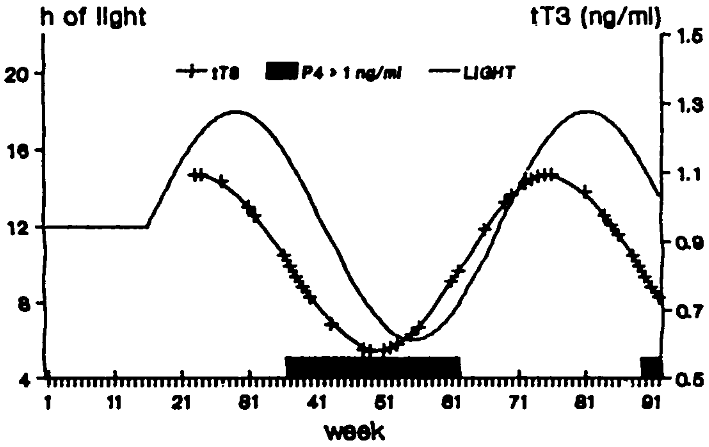
Group B, artificial sinusoidal pattern, the reverse of natural light.

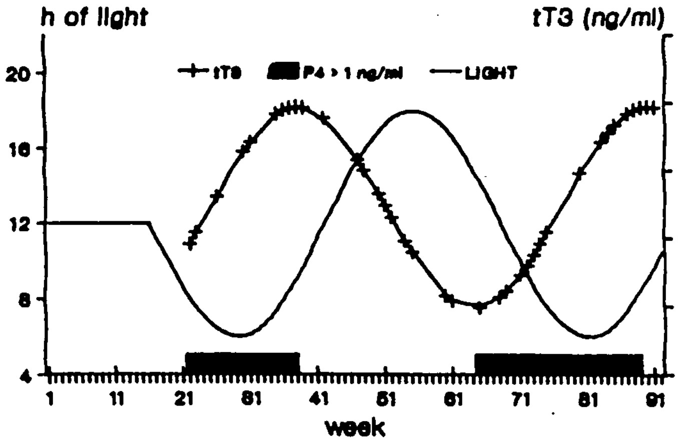
Group C, artificial sinusoidal pattern, closely mimicking natural light. (artificial summer and winter solstices for Groups B and C were 18L:6D and 6L:18D, respectively.)

Group D, natural light pattern, 53.5° N latitude

Figure IV.1A. Light patterns, predicted total T3 curves for group averages of each photoperiodic group and estrous cycles (periods of P4 > 1 ng/ml for 50% of ewes in each photoperiodic group)


Group A (constant 12L:12D)


Group B (artificial light)


Group C (artificial light)

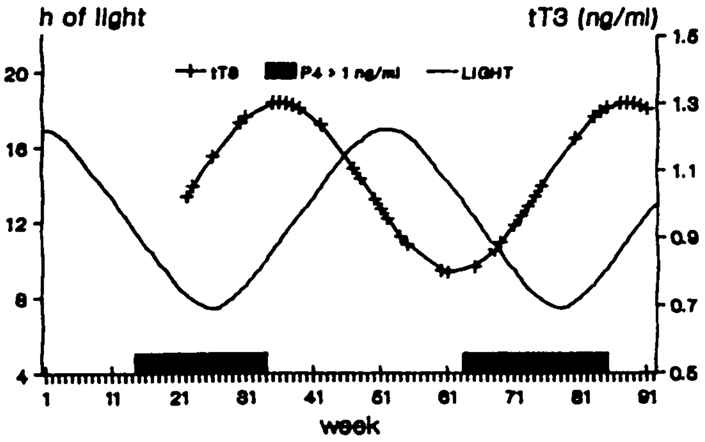
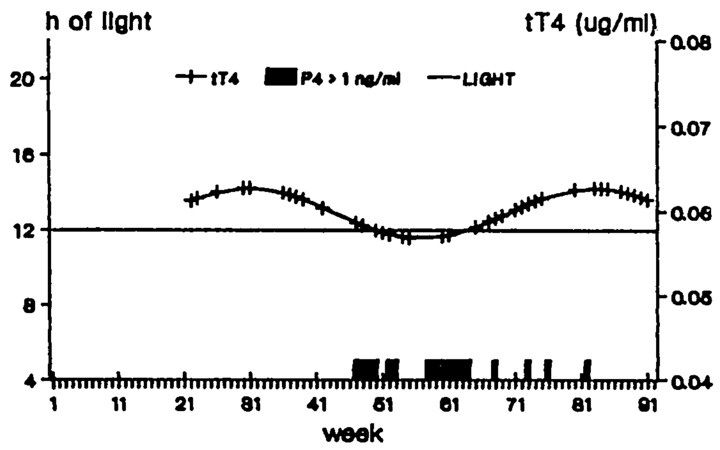
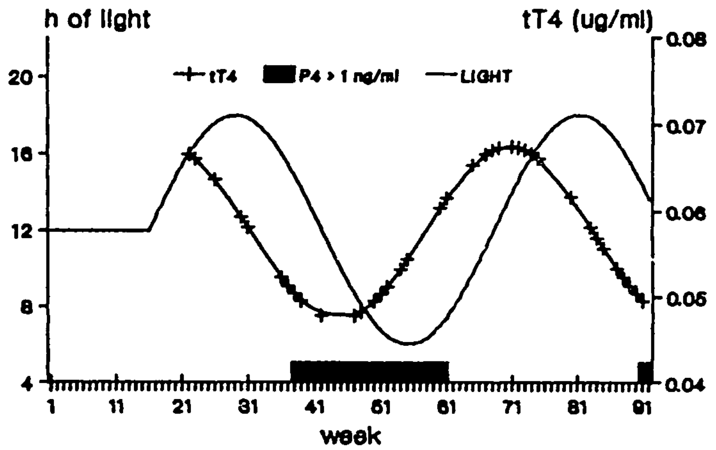

Group D (natural light)

Figure IV.1B. Light patterns, predicted total T4 curves for group averages of each photoperiodic group and estrous cycles (periods of P4 > 1 ng/ml for 50% of ewes in each photoperiodic group)

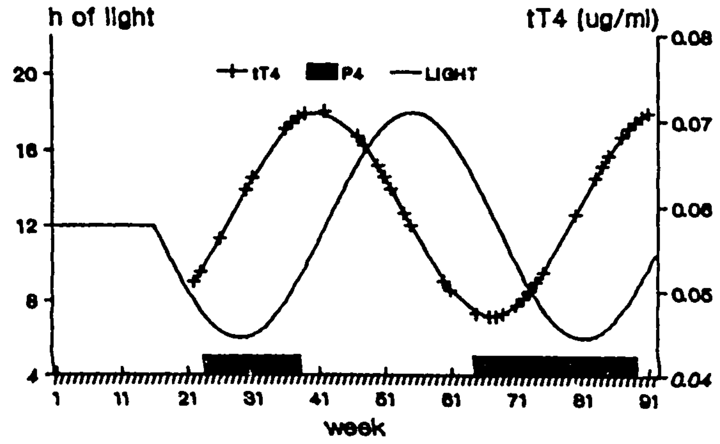
Group A (constant 12L:12D)



Group B (artificial light)



Group C (artificial light)



Group D (natural light)

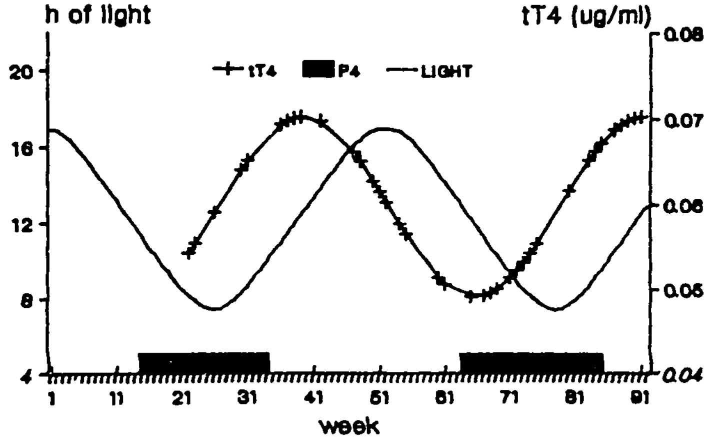
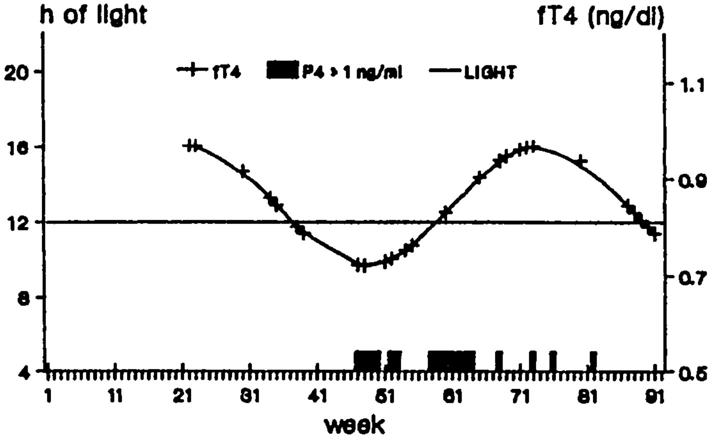
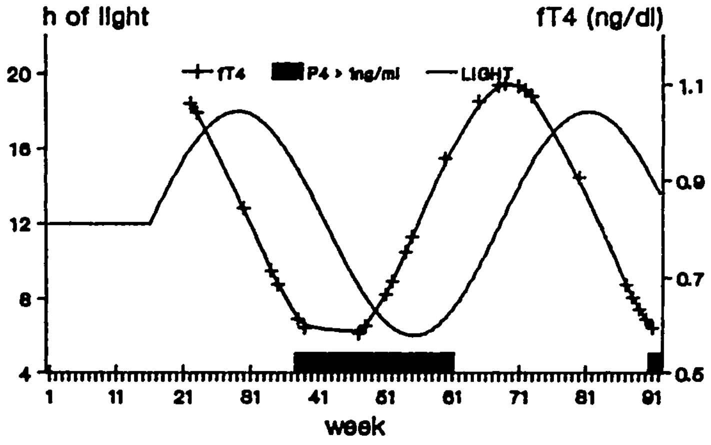


Figure IV.1C. Light patterns, predicted free T4 curves for group averages of each photoperiodic group and estrous cycles (periods of P4 > 1 ng/ml for 50% of ewes in each photoperiodic group)

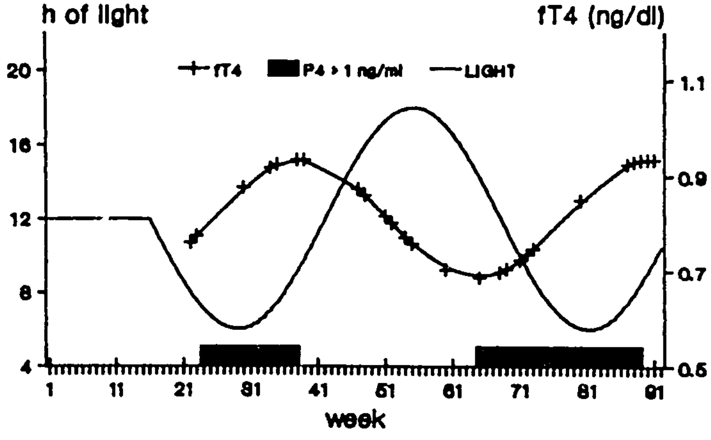
Group A (constant 12L:12D)



Group B (artificial light)



Group C (artificial light)



Group D (natural light)

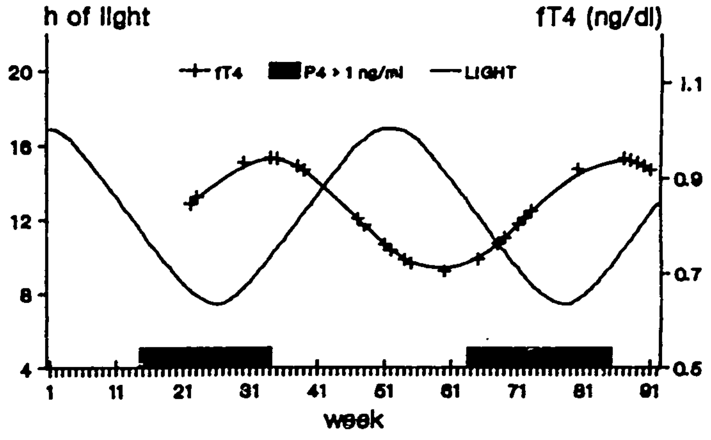
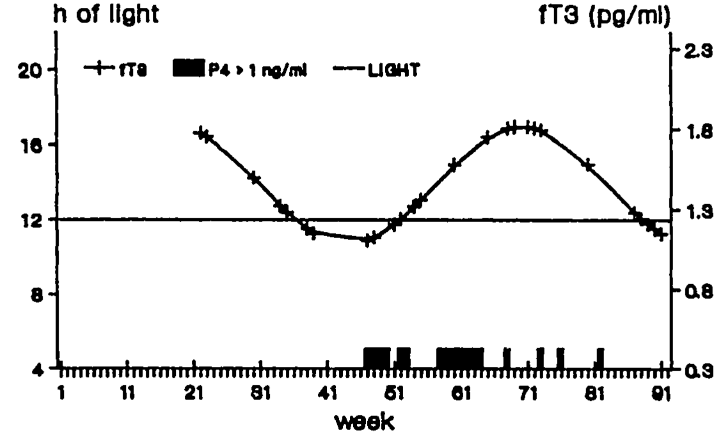
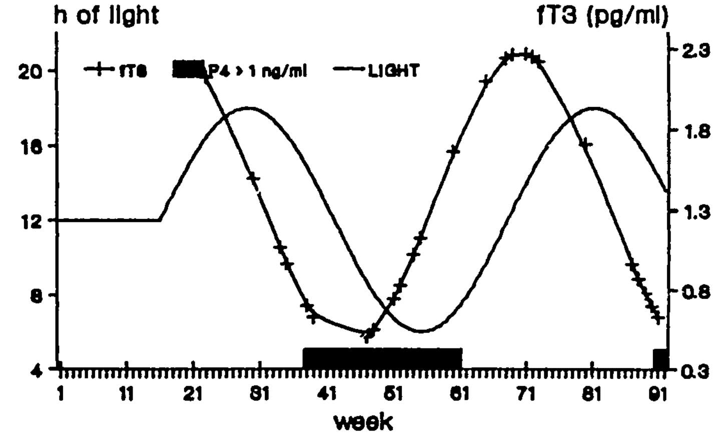


Figure IV.1D. Light patterns, predicted free T3 curves for group averages of each photoperiodic group and estrous cycles (periods of P4 > 1 ng/ml for 50% of ewes in each photoperiodic group)

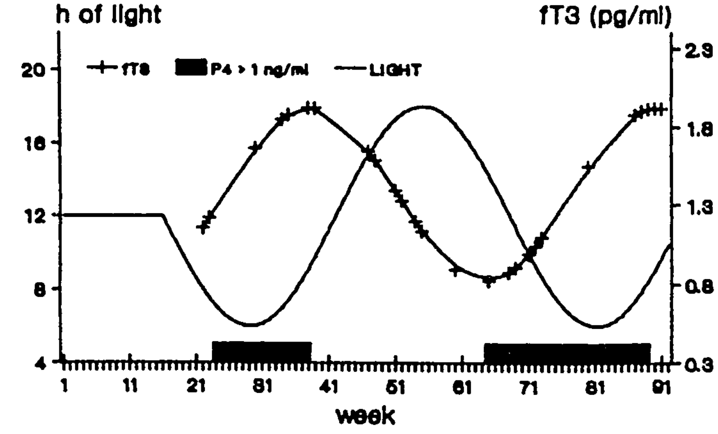
Group A (constant 12L:12D)



Group B (artificial light)



Group C (artificial light)



Group D (natural light)

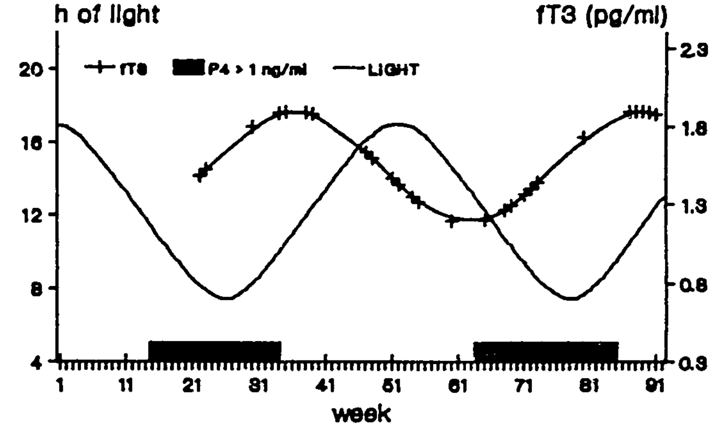
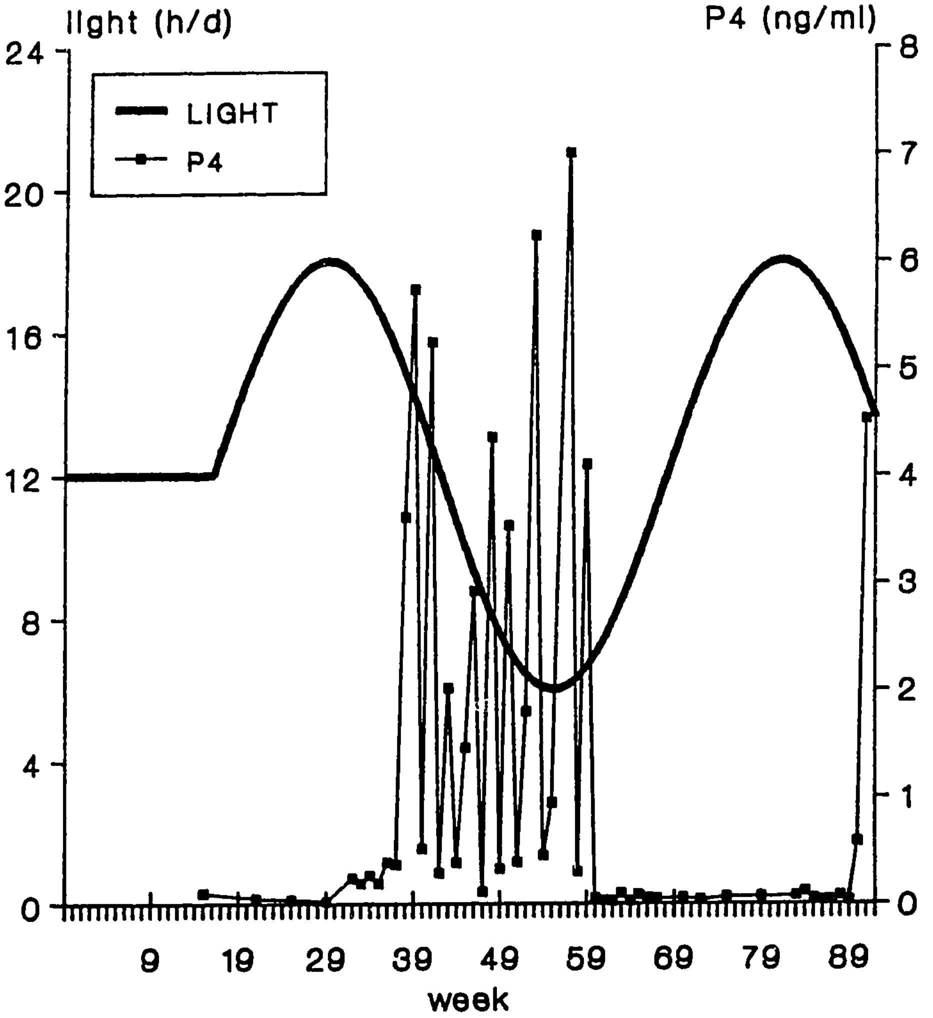


Figure IV.2. Progesterone profile (P4) for ewe #81 (group B) exposed to an artificial light pattern.



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V. INFLUENCE OF PHOTOPERIOD ON THE VOLUNTARY FOOD INTAKE AND METABOLIC HEAT PRODUCTION OF EWES

INTRODUCTION

Seasonal photoperiod has long been known to influence the physiology and behaviour of animals (Brady, 1982). In temperate and polar regions of the world, many animals must adapt to the natural seasonal variations in the quality and quantity of food available (Kay, 1985). In order to survive periods of winter scarcity, animals have developed adaptive physiological strategies. Seasonal patterns in intake have been observed in domestic sheep (Gordon, 1964; Blaxter et al., 1982) and wild ungulates (Milne et al., 1978; Ryg and Jacobsen, 1982; Loudon et al., 1989). The general pattern observed for intake is a maximum during spring and summer and a decline during the fall and winter. This pattern persists even when food is provided in abundance throughout the seasons. Changes in daylength have been shown to modify food consumption in domestic sheep and deer (Kay, 1979; Simpson et al., 1984). The experimental utilization of two cycles of daylength changes in one year elicited two distinct cycles in food intake for both deer and sheep (Simpson et al, 1984).

However, voluntary food intake is a complex process which is influenced by a variety of factors both internal and external to the animal. These factors influencing and regulating food intake of ruminants are detailed in reviews by Weston (1982), Young (1987), and Grovum (1988). One primary factor regulating appetite is the physiological status of the animal, with the energy balance attributed as being a central driving force. Although photoperiod is one external cue which serves to entrain the seasonal cycle in food intake, other physiological demands may have a more predominant influence (Young, 1987).

Previous photoperiodic studies (Chapter II) demonstrated a distinct metabolic heat production (MHp) pattern for ewes in relation light changes, but independent of food intake, which was held constant. If, as has been suggested, energy requirements drives food intake, then with *ad libitum* feeding a cyclic pattern would be expected for food intake. The purpose of the present study, was to examine the food intake response of ewes previously entrained to varying light regimens.

MATERIALS AND METHODS

Animals, diet and management

Nineteen Suffolk ewes approximately 2.5 years of age were utilized in the trial. They were caged in metabolism crates for individual feeding, in one of four photoperiodic environments to which they had been exposed for the previous 79 weeks and had been fed a near maintenance diet of a 600 g pelleted barley based concentrate and 200 g brome/alfalfa hay.

The ewes were gradually offered increasing amounts of a pelleted alfalfa based concentrate with 300 g of the previously fed pelleted barley based concentrate and 200 g hay, for two weeks prior to *ad libitum* feeding, to avoid problems in digestive function. Following this transition period, the ewes then received the pelleted alfalfa based concentrate *ad libitum* and 200 g of chopped brome/alfalfa hay daily. The crude protein (CP) and metabolizable energy (ME) content of the pellets and hay, on a dry matter basis, were 16.5%, 8.8 MJ/kg and 15.0%, 9.2 MJ/kg, respectively. The ewes received this diet for a further 32 weeks. Free access to water and trace-mineralized salt was provided throughout the experiment.

Experimental design

The ewes had previously been randomly assigned to one of four photoperiodic environments. All groups began the trial while exposed to approximately 12 h daily light. Group A were maintained in constant 12L:12D. Group B were exposed to an artificial sinusoidal light pattern with an initial decrease in daily light. Group C were exposed to the reverse artificial sinusoidal light pattern of group B and closely mimicked the natural seasonal light pattern. The type of lighting and photointensity are detailed in chapter II. Group D were maintained in a windowed area and exposed to the natural seasonal light pattern experienced at 53.5° N latitude. At the start, natural daylight experienced by this group was 13.5 h. Photointensity varied daily with season and climatic conditions for group D. The light patterns for all groups are shown in Figure V.1. The final 15 weeks of the constant feeding trial are included to demonstrate the previous photoperiod exposure.

Experimental procedures and measurements

Records were kept of daily voluntary food intake (VFI); refusals were weighed back each day and the amount of food given was adjusted to give a refusal of approximately 300 g per day. Ten day digestibility trials were conducted after 7 and 25 weeks of *ad libitum* feeding, for the determination of dry matter (DM) digestibility of the diet. Live weight was recorded weekly for each ewe.

Metabolic heat production (MHp) values were determined by indirect calorimetric measurements. The oxygen consumption was measured utilizing a ventilated hood apparatus which enclosed the animals head. The utilization of the hood technique over the water bath technique (utilized in the constant feed trial) relates to *ad libitum* feeding, whereby a set measurement time during a 24 h period could not be established which would be equivalent between animals because of the variation between ewes in their times eating and ruminating. Measurements were therefore done on each sheep for a 24 h period, once every 4 weeks during the first 16 weeks of the trial and once during the final 3 weeks of the trial. The daily average MHp was calculated from the rate of ventilation (V_o) (approx. 125 L/min) and oxygen concentrations (O_i and O_o) using the equation of McLean (1972).

$$MHp = 20.47\ V_o\ (O_i - O_o)$$

Oxygen concentrations were measured using a dual-channel paramagnetic analyzer (Taylor Servomex OA 184). These data were recorded and stored for later processing and analyses using an electronic Datataker (model DT100, Data Electronics, Box Hill, Vic., Australia). This system was calibrated every 4 weeks using the iron burner technique of Young et al (1984). The calculated daily average MHp value was utilized as the estimate of MHp for the animal.

Statistical analyses

Analysis of variance was done using the General Linear Models procedures (SAS, 1988) for DM digestibility, food intake, liveweight and estimated liveweight gain. Food intake (total and per $kg^{.75}$ liveweight) and liveweight were analyzed in three periods, these being, the first 10 weeks, the second 10 weeks and the final 12 weeks of *ad libitum* feeding. Overall treatment differences were established using the error term of sheep nested within treatment. The significance of the mean differences were determined using a t test equivalent to the Fisher's least-significant-difference (LSD) test.

Linear regressions were fitted to intake (total and per $kg^{.75}$ liveweight) versus week for the period of declining intake for each ewe. Linear regression analysis was also conducted for MHp ($MJ/kg^{.75}/d$) versus intake ($MJ/kg^{.75}/d$), with the inclusion of the values for the final measurement taken during the restrict feeding trial. Analysis of variance of the computed slopes of the regression lines was done to examine treatment effects. The significance of the mean differences were then compared using the t-test (LSD). Values are given are means ± standard deviations (SD) unless otherwise specified. Significance was assessed at $P<0.05$ unless otherwise stated.

RESULTS

During the first 2 to 3 weeks of *ad libitum* feeding, 2 sheep in group B had periods of inappetence which were related to bloat. Later during the trial, 2 sheep from groups A and C also displayed one or two periods of inappetence lasting 2 to 3 weeks. In one case bloat was evident, however, in the other cases there appeared to be other health problems related to leg problems. To avoid possible confounding effects related to this, data from those sheep afflicted at this stage were not included in the analysis.

There were no significant differences between groups or with time in the dry matter digestibility of the diet, with an overall average digestibility of 49.8 ± 2.4%. This was significantly lower than the average dry matter digestibility (75.7 ± 2.8%) for the previous restrict feeding period.

The pattern of food intake is illustrated in Figure V.1. The general pattern displayed for groups A, C and D, involved an initial increase to a maximum average intake of about 3572 g/d during the first 4 to 8 weeks, followed by a continual decline for the remaining weeks (Figure V.1A). Group B had a similar increase (maximum average intake of 3390 g/d), followed by a decrease in VFI until approximately week 10, at which point intake plateaued, at an average of 2600 to 2900 g/d.

During the initial two 10 week periods of *ad libitum* feeding, there were no significant differences between the photoperiodic treatment groups in absolute VFI or intake expressed per kg body weight $^{.75}$. Absolute VFI during the final 12 weeks was significantly greater for the ewes exposed to artificially increasing daily light at this time (group B) than for the ewes in the reverse natural light or constant light (Table V.1). The intake of group B was on average 23% and 26% greater than groups A and D, respectively. Group C had an average intake 17% lower than group B, although this was not significant. In addition, groups C and D were highest (not significant) at peak intake, which coincided with increasing daylength for these groups.

The average rate of decline, (as estimated from the slopes for the regressions), in absolute (total) intake for the ewes in group B (11.1 g/week), was significantly lower than that for the ewes exposed to the reverse artificial and natural light pattern (decline of 45.2 and 63.7 g/week, respectively). The ewes in constant light had an intermediate decrease in total intake of 38.5 g/week (Table V.2).

At the start of the experiment, the ewes maintained previously in constant light were significantly heavier (64.1 kg) than those exposed to seasonally changing light (58.9 kg). Liveweight increased in a similar manner for all groups and began to stabilize following 15 to 20 weeks of *ad libitum* feeding (Figure V.1). The ewes in constant light (group A) remained significantly heavier for the first 20 weeks, than the ewes initially in artificially decreasing light (group B) and those in natural light (group D) for the first 10 weeks (Table V.1). Similarly estimated liveweight gain was significantly greater for group D in comparison to group A during the initial 10 weeks (Table V.1). Differences in liveweight had been eliminated by the final 12 weeks (Table V.1), although group B had a significantly greater liveweight gain than group D at this time.

MHp values followed a pattern similar to that of VFI with a peak value occurring for all groups during the initial 4 to 8 weeks of *ad libitum* feeding and then declining over time. No significant differences were observed between groups during the initial 10 weeks (Table V.1). However group B had a significantly greater daily MHp than groups C and D for the final measurement taken during weeks 29 to 31, which coincided with the higher food intake observed for group B at this time. MHp ($MJ/kg^{.75}/d$) was directly related to food intake ($MJ/kg^{.75}/d$) for all groups ($r=0.93$, $P < 0.001$) (Table V.2). The regression lines depicting this relationship are shown in Figure V.2, whereby values for all ewes in each group have been plotted for MHp ($MJ/kg^{.75}/d$) and energy retention (determined as difference between intake and MHp) against food intake ($MJ/kg^{.75}/d$).

DISCUSSION

A photoperiodic influence became increasingly prominent during after 20 of weeks of *ad libitum* feeding, at which time ewes exposed to increasing daily light (group B) had a greater intake than ewes in the reverse natural (group D) and constant light (group A) pattern. A more subtle influence was evident during initial *ad libitum* feeding, with groups C and D having greater intakes coinciding with the time of exposure to peak daylengths. Group C had peaks and nadirs in light approximately 4 weeks later than the natural light group. Therefore during the final weeks of the study, group D had been exposed to a decreasing daylength for a greater period and light changes had almost reached the naturally shortest day. This may account for group C having a higher intake than group D, such that in the natural environment minimum intakes of sheep have been found to occur from December to February, coinciding with the time of minimum and initially increasing daylength (Gordon, 1964). Maximum intakes are generally evident from June to August, coinciding with the time of maximum and initially decreasing daylength (Gordon, 1964).

Present results confirm that seasonal photoperiod serves as a modifier of VFI, though other factors may have a more marked influence such as the drive for attainment of genetic body size. This was evidenced by the similarity in the pattern of VFI during the initial 20 weeks irrespective of the light regimen imposed. In a comparison of 30 kg ewes fed *ad libitum* in January or July, Blaxter et al. (1982), found that no seasonal differences in intake since at low body weights the effect of daylength cannot nullify a presumptive effect of body size on VFI. Once inherently determined maximum body size is attained, photoperiod influences on food intake become more evident.

These results provide evidence in support of the model outlined by Young (1987), in which long term genetically determined requirements involving the energy balance of the animal must be satisfied before modifiers such as photoperiod will have an influence. Once this energy balance has been established, fluctuations in intake occur around a consistent level which is characteristic of that animal.

Although the ewes in the present study had stabilized at an equilibrium weight of approximately 60 kg prior to *ad libitum* feeding, this was below their potential 'mature' weight. Suffolk sheep are a large framed breed, with ewes having a potential mature body weight of 77 to 90 kg (Scheer, 1985). In the present trial, differences in intake related to the photoperiodic environments became evident after the ewes had attained a new stable weight of 85 to 90 kg.

An initial increase in feed intake observed for all groups may also be a response to a new feed source. Foot and Russel (1978) observed a similar pattern in mature Scottish Blackface ewes, which were brought indoors in November, and given one of three roughage diets. Intake increased to a maximum after 3 to 6 weeks and then fell sharply (by approximately 25 to 50% of maximum) for the following 6 to 8 weeks for all the diets (Foot and Russel, 1978). A sharp decline was not observed in this study, which may reflect seasonal photoperiod differences. The sharp decline in the study of Foot and Russel (1978), may have been reinforced by exposure of the sheep to natural decreasing daylength. In the present study, the reverse photoperiodic situation existed for groups C and D, and exposure of these ewes to long daylengths may have contributed to the more gradual decline (Figure V.1). The slower rate of decrease in intake observed for group B, also likely reflects the influence of photoperiod. Following adjustment to the feed and stabilization of body weight, intake for group B stabilized, at the period of increasing daylength, while intake of the other groups continued to decline, with decreasing daylength.

The response observed for group A in constant light should solely reflect the effects related to diet change and physiological status of the sheep. This was evidenced by the intermediate decline in intake between group B and the two groups in the reverse light pattern (C and D). Exposure of the ewes to decreasing photoperiod served to reinforce the downward trend in intake (groups C and D) whereas exposure of ewes to increasing photoperiod resulted in a stabilization of intake (group B). Therefore, the initial intake pattern observed for all groups was related to the transition from maintenance to *ad libitum* feeding and the fat and protein balance of the ewes.

The good correlation between MHp (or energy retention) and food intake was as expected, as this relationship has been well documented (Webster, 1983). This increase in MHp with increased food intake is referred to as the heat increment of feeding and relates primarily to the energetic inefficiency of the reactions by which absorbed nutrients are metabolized as well as the heat production associated with eating and rumination, microbial fermentation and metabolic activities in the gut (Webster, 1983). The response observed in the present study was one in which each successive increase in ME intake produced an equivalent increment in MHp (Figure V.2). Generally, two linear slopes are utilized to describe the relationship between energy intake and energy retention, with the assumption that the efficiency of utilization is less above maintenance feeding (zero energy retention) than below maintenance (McDonald et al., 1981).

This known relationship between food intake and metabolic heat production has made it difficult to separate the factor cued directly by photoperiodic changes. It has been shown that photoperiod directly influences food intake in certain ruminants (Kay, 1979; Simpson et al., 1984). The close correlation between MHp and food intake provides evidence that food intake directly drives MHp. However previous evidence from this study demonstrated a photoperiodic influence on metabolism, independent of changes in food intake (Chapter II). Therefore present findings of both the food intake and photoperiodic effects on MHp, are suggestive of a combined influence whereby photoperiod serves to prime or adjust the metabolic system at the time of increasing availability of feed in the natural environment situation. This causes an initial stimulation in appetite and food intake and would subsequently serve in a positive feedback manner increasing MHp and subsequently greater intake, until the point at which parameters such as body fat reserves (necessary for winter periods of food scarcity) are replenished. This photoperiodic influence may provide an explanation for the group in decreasing daylength having a higher incidence of digestive problems and inappetence during the initial weeks of *ad libitum* feeding, as they would have a decreasing metabolism at this stage and may therefore not be physiologically primed for such increases in food intake.

As mentioned, control of VFI is complex and involves the interaction of many different parameters. The assessment of the importance of physiological and environmental factors is often difficult. Only with an understanding of how these parameters function and interrelate can effective and economical feeding schemes be developed.

From this study, it is evident that a number of factors may influence the VFI of ewes. The effects of the initial body condition of the ewes was found to be of primary importance to intake during the initial period. A photoperiodic influence however, became increasingly evident, once mature size had been attained, such that the group in long daylengths have a greater intake than the other groups in the final weeks of the trial. Further studies of an extended duration may help determine the degree of fluctuation in intake and the precise time of peaks and nadirs in intake, in relation to photoperiod, for ewes of this breed.

In conclusion, this study lends support to the hypothesis of the energy and protein balance being a primary determinant of voluntary food intake, with photoperiod serving to modify intake once this inherently determined body size is established and also serving to adjust the metabolic system for changes in intake.

Table V.1 - Group averages of ewes exposed to various photoperiodic environments, for total food intake, food intake expressed as a ratio of group A, liveweights, liveweight gain, and MHp, for 3 periods of *ad libitum* feeding.

	Weeks of *ad libitum* feeding		
	1 to 10	10 to 20	21 to 32
A. Food intake (g/d)			
Group A	$3036^{a} \pm 29$	$2595^{a} \pm 25$	$2314^{a} \pm 27$
Group B	$3009^{a} \pm 32$	$2882^{a} \pm 26$	$2846^{b} \pm 33$
Group C	$3256^{a} \pm 36$	$3035^{a} \pm 29$	$2436^{ab} \pm 37$
Group D	$3336^{a} \pm 36$	$2961^{a} \pm 29$	$2175^{a} \pm 32$
B. VFI expressed as ratio of group A (12L:12D)			
Group A	$1.00^{a} \pm 0.01$	$1.01^{a} \pm 0.01$	$1.00^{a} \pm 0.01$
Group B	$0.95^{a} \pm 0.01$	$1.08^{a} \pm 0.02$	$1.17^{b} \pm 0.02$
Group C	$1.03^{a} \pm 0.01$	$1.12^{a} \pm 0.02$	$0.98^{a} \pm 0.02$
Group D	$1.05^{a} \pm 0.01$	$1.10^{a} \pm 0.02$	$0.94^{c} \pm 0.02$
C. Liveweight (kg)			
Group A	$73.9^{a} \pm 0.2$	$88.0^{a} \pm 0.2$	$89.7^{a} \pm 0.2$
Group B	$69.1^{b} \pm 0.2$	$83.0^{b} \pm 0.2$	$92.4^{a} \pm 0.2$
Group C	$71.1^{ab} \pm 0.3$	$86.4^{ab} \pm 0.2$	$92.1^{a} \pm 0.3$
Group D	$69.8^{b} \pm 0.3$	$87.0^{ab} \pm 0.2$	$92.1^{a} \pm 0.2$
D. Estimated liveweight gain (kg/week)			
Group A	$1.67^{a} \pm 0.09$	$0.38^{a} \pm 0.14$	$0.51^{ab} \pm 0.10$
Group B	$1.89^{ab} \pm 0.12$	$0.83^{a} \pm 0.20$	$0.78^{a} \pm 0.14$
Group C	$1.92^{ab} \pm 0.11$	$0.56^{a} \pm 0.17$	$0.45^{ab} \pm 0.12$
Group D	$2.06^{b} \pm 0.11$	$0.63^{a} \pm 0.17$	$0.18^{b} \pm 0.12$
E. Metabolic heat production (MJ/kg$^{.75}$/d)			
Group A	$0.65^{a} \pm 0.03$	$0.53^{a} \pm 0.02$	$0.47^{ab} \pm 0.02^{*}$
Group B	$0.64^{a} \pm 0.03$	$0.57^{ab} \pm 0.03$	$0.54^{a} \pm 0.03^{*}$
Group C	$0.69^{a} \pm 0.03$	$0.63^{b} \pm 0.03$	$0.42^{b} \pm 0.04^{*}$
Group D	$0.66^{a} \pm 0.03$	$0.56^{ab} \pm 0.03$	$0.38^{b} \pm 0.03^{*}$

Values given as least square means ± standard error of mean (SEM)

* value is estimate of measurements taken during weeks 29-31

^{a,b,c} means with different superscript in a column differ ($P<0.05$)

Group A, constant 12L:12D

Group B, artificial sinusoidal light pattern, reverse of natural light

Group C, artificial sinusoidal light pattern, closely mimicking natural light
(artificial summer and winter solstices; 18L:6D and 6L:18D, respectively)

Group D, the natural seasonal light pattern (53.5°N latitude)

Table V.2. Coefficients of determination (R^2), slopes, and intercepts of linear regressions between food intake and week, and between food intake and MHp, for each photoperiod regimen.

	Intercept	Slope	R^2
A. Food intake (g DM/d) vs week			
Group A	3031^{a} ± 207	-38.5^{a} ± 9.5	-0.56
Group B	3049^{a} ± 227	-11.1^{b} ± 10.4	-0.18
Group C	3501^{a} ± 253	-45.2^{a} ± 11.6	-0.80
Group D	3685^{a} ± 253	-63.7^{a} ± 11.6	-0.92
B. Food intake (MJ/kg$^{.75}$/d) vs MHp (MJ/kg$^{.75}$/d)			
Group A	0.157^{a} ± 0.02	0.472^{a} ± 0.03	0.87
Group B	0.166^{a} ± 0.03	0.447^{a} ± 0.03	0.87
Group C	0.172^{a} ± 0.03	0.467^{a} ± 0.04	0.89
Group D	0.197^{a} ± 0.03	0.389^{a} ± 0.04	0.94
C. Food intake (MJ/kg$^{.75}$/d) vs MHp (MJ/kg$^{.75}$/d)			
Group A	-0.157^{a} ± 0.02	0.528^{a} ± 0.03	0.89
Group B	-0.166^{a} ± 0.03	0.558^{a} ± 0.03	0.92
Group C	-0.172^{a} ± 0.03	0.533^{a} ± 0.04	0.91
Group D	-0.197^{a} ± 0.03	0.613^{a} ± 0.04	0.97

values are given are least square means ± standard error of the mean

^{a,b} means with different superscript in a column differ ($P<0.05$)

Group A, constant 12L:12D

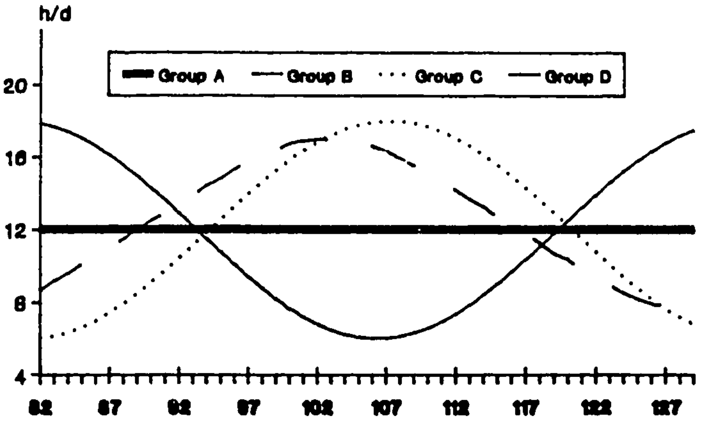
Group B, artificial sinusoidal pattern of light, reverse of natural light

Group C, artificial sinusoidal pattern of light, closely mimicking natural light (artificial summer and winter solstices of 18L:6D and 6L:18D, respectively)

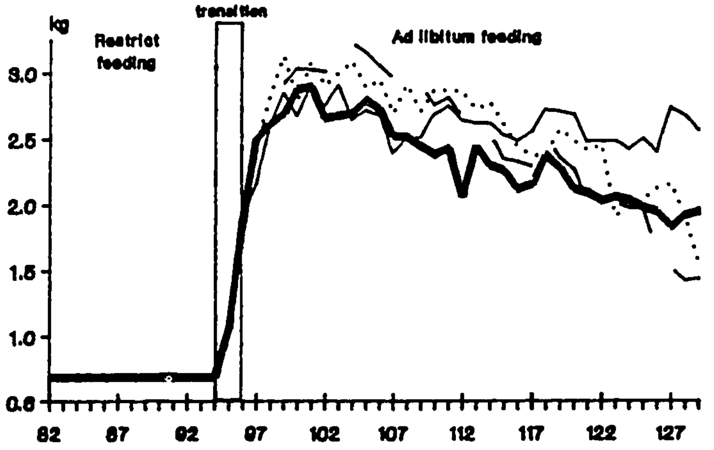
Group D, natural seasonal light (53.5°N latitude)

Figure V.1. Photoperiod regimens and group averages for weekly dry matter intake and liveweights

A. Light Patterns



B. Dry Matter Intake



C. Liveweight changes

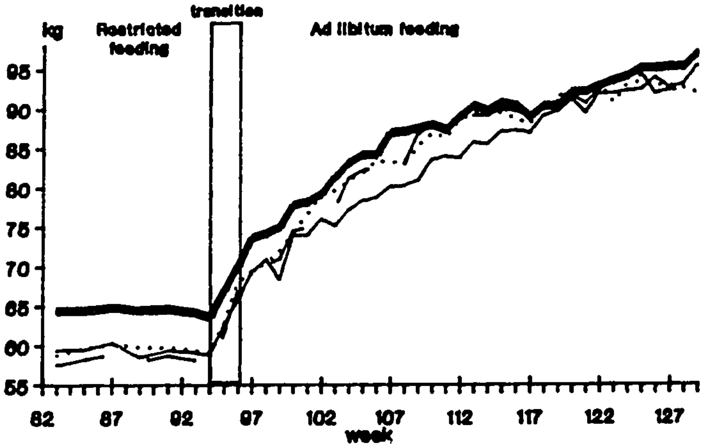
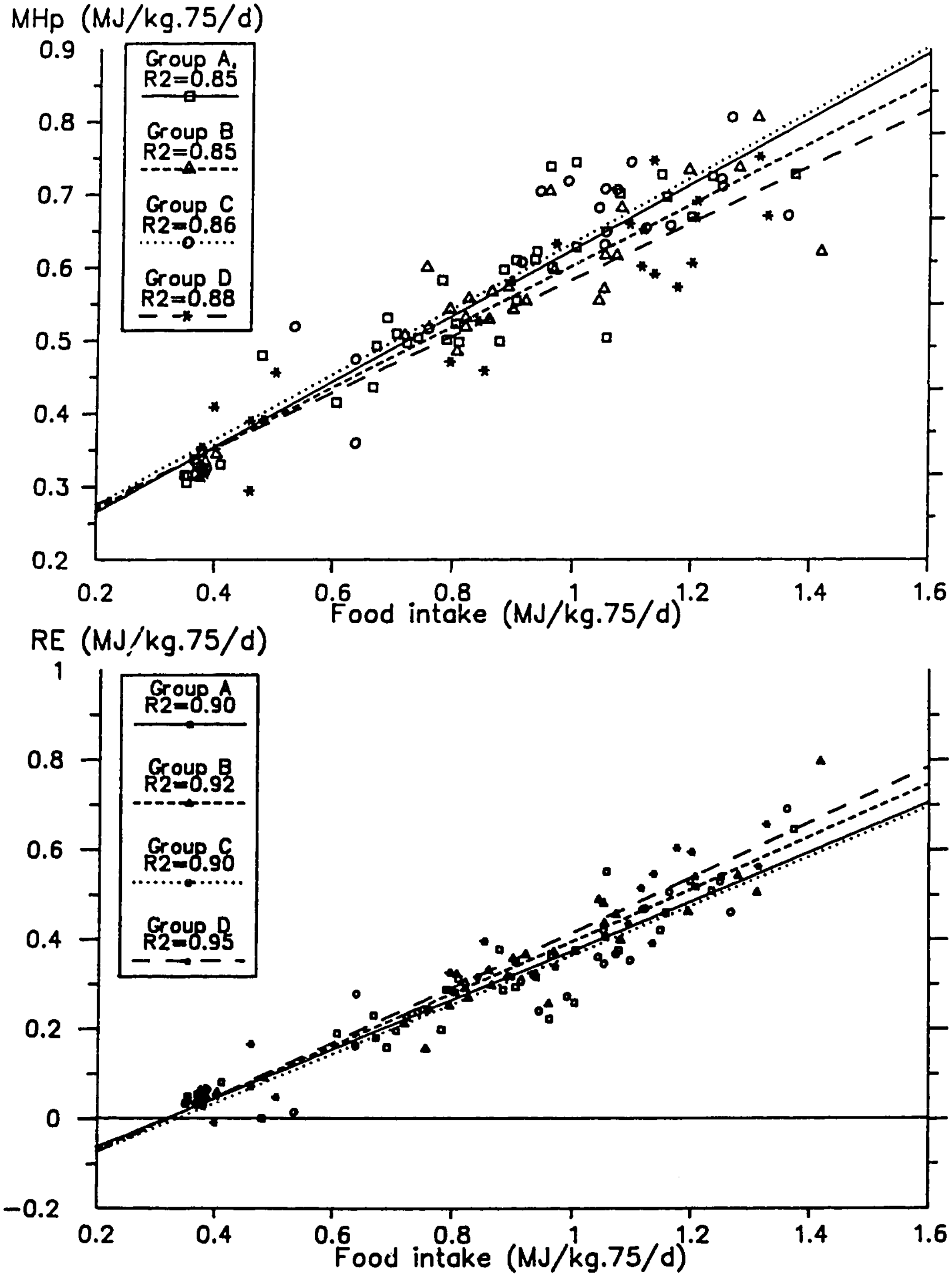


Figure V.2. Metabolic heat production (MHp) and energy retention (RE) with voluntary food intake (MJ/kg.75/d) and the calculated regression line



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VI. INFLUENCE OF PHOTOPERIOD ON THE ACTIVITY OF CONFINED SHEEP

INTRODUCTION

Seasonal changes in metabolic heat production (MHp) have been observed in a variety of animals. Generally metabolic heat production decreases in the fall and winter and increases during spring and summer. There is an energy cost associated with physical activities such as standing, eating and associated feeding activity, and grooming (Toutain et al., 1977). One activity shown to contribute to the seasonal variation in heat production is changes in voluntary food intake. However, Blaxter and Boyne (1982) found a change in MHp that was independent of food intake. Current research (chapter II) supports Blaxter and Boyne (1982) observations, in that seasonal changes in MHp were observed in ewes corresponding to controlled patterns of artificial and natural seasonal light. The seasonal pattern observed, involved an increase in MHp with increasing daily light and a decrease in MHp with decreasing daily light. Casual visual observations of the sheep exposed to the seasonal light patterns indicated possible variations in their behaviour, with apparent increases in activity with increased daily light. Changes in observable physical activities may contribute to the seasonal variation observed in MHp. Head movement patterns have been suggested to be a reasonably reliable indicator of excitability and have been utilized by Kondo and Hurnik (1988) in an assessment of dairy cow behaviour.

The present study was conducted to determine if seasonal variations in the behaviour of confined sheep, as measured by particular physical activity parameters, could account for some of the variation in MHp induced by seasonal light patterns. Changes in physical activity were also examined in relation to food intake and subsequent liveweight changes of the animals.

MATERIALS AND METHODS

Animals, Housing and Management

The twenty-two Suffolk ewes utilized for measurements of activity were involved in a study examining photoperiodic effects on MHp with restricted feeding (Chapter II). A second period of activity measurements was conducted during a continuation of the energy metabolism study which involved *ad libitum* feeding and measurements of voluntary feed intake (Chapter V). The ewes were approximately 2 years of age at the start of the activity measurements and had been continuously exposed to their respective light environments for the previous 57 weeks. The ewes were caged in metabolism crates to allow for individual feeding and fecal collections. Detail of the feeds and feeding schemes for the restrict fed and *ad libitum* trial are given in Chapters II and V, respectively.

xperimental Design

The ewes had previously been randomly assigned to one of four light environments. The ewes in group A were maintained in constant daily 12 h light (12L:12D) throughout the trial. The ewes in group B were exposed to an artificial sinusoidal light pattern the reverse of natural light. The ewes in group C were exposed to the reverse artificial light pattern of group B, and this closely mimicked natural seasonal light with a lag of 4 weeks. The artificial summer and winter solstices, for group B and C were 18L:6D and 6L:18D, respectively. Detail of artificial lighting is provided in Chapter II. The ewes in group D were exposed to the natural seasonal light pattern experienced at 53.5° N latitude, with photointensity varying daily with season and climatic conditions. At the start of the activity measurements the ewes were all exposed to approximately 12 h of daily light. The light patterns experienced during the final 57 weeks of the main study are shown in Figure VI.1. The boxes (1 through 7) below the light patterns represent the periods of activity measurements.

Experimental measurements

Activity of the ewes was evaluated through transducers to monitor head movements, time spent standing and lying, and (during the *ad libitum* feeding period of the study), the number and pattern of jaw movements.

Side to side (SS) and up and down (UD) head movements were measured utilizing 2 mercury switches attached to a halter placed on the head of the animal. The output from the transducers were compiled on a portapac Datataker model DT100 (Data Electronics, Box Hill, Vic., Australia), and the number of activities were counted and recorded every 6 minutes in each 24 h period. For examination of daily patterns the counts were summed over 30 minute periods and for statistical analysis for comparison between groups the daily total for each recording day was utilized.

To determine the amount of time spent standing and lying a narrow piece of flexible rubber was secured loosely around the girth of the animal and an elastic was attached from this rubber strip to a microswitch located approximately 1 m above the back of the animal. When the animal lay down, the elastic band pulled down, the switch was closed and the event recorded. Recordings were taken every 2 minutes and estimates for 30 min intervals and daily totals were calculated as described for head movements.

Measurements of number of jaw movements were taken using a microswitch attached to the halter at the cheek region which was connected to a flexible wire positioned underneath the jaw of the ewes. The number of jaw movements were recorded every 6 minutes and estimates of number of movements every 30 minutes and daily totals were calculated as described for head movements. Rumination times were estimated from periods of repeated consistent jaw movement values, generally coinciding with times when the animals were lying down. An estimate was obtained of the time spent ruminating each day.

Statistical analyses

Analysis of variance was done using the General Linear Model (GLM) procedures (SAS, 1988) for each activity for 24 h totals, the number per min of light, number per min of dark and the ratio of number/min light to number/min dark. Overall treatment differences were established using the error term of sheep nested within treatment. The significance of the mean differences were determined using a t test equivalent to the Fisher's least significant-difference (LSD) test.

The Kolmogorov-Smirnov (KS) two-sample test (which tests whether two samples may reasonably have come from the same distribution (Steel and Torrie, 1980)), was utilized to compare the daily patterns of the standing for the treatment groups.

Relationships between activities and hours of light experienced, MHp and liveweight were examined by regression analyses. Significance was assessed at $P<0.05$ unless otherwise specified.

RESULTS

One ewe died during the initial period of activity measurements. Two ewes were removed from the experiment at the end of the restricted feeding trial for reasons unrelated to the experimental treatments imposed. Data collected from these ewes up until their time of removal, were utilized in the statistical analyses.

Daily activity patterns

All ewes exhibited a regular daily pattern of activities as shown in Figure VI.2, during the restricted feeding period. This daily pattern consisted of an increase in activity 1 to 2 hours prior to feeding, a peak during feeding and an elevation for 2 to 4 hours following feeding. This elevation was of greater duration for both SS head movements and standing duration in comparison to UD head movements. An increase in standing duration was also prominent but of lower magnitude from 0500 to 1000 h (Figure VI.2). The daily standing pattern was not significantly different between treatment groups during periods 1 to 3 of restricted feeding.

The average daily pattern during *ad libitum* feeding was similar to that observed during restrict feeding but with a reduced peak in activities from 1200 to 1800 h daily (Figure VI.2). The average daily standing patterns for groups B and C, which were in reverse artificial light patterns, are shown in Figure VI.3, for measurement periods 4 and 5. There was a significant difference ($P<0.01$) in the standing pattern of group B in comparison to groups C and D during period 4. Similarly, the daily total and the proportion in the light phase were found to be significantly greater for group B at this time in comparison to groups C and D. Groups B and C also had a significantly different pattern (P<0.01) during period 5. Although there was no difference between these groups in the total time spent standing per day (Table VI.1), there was a difference in the proportion of time standing in the light phase of the day with group B being significantly greater.

The general daily pattern for jaw movements observed for the *ad libitum* feeding periods were similar to the pattern for standing. A peak in number of jaw movements resulted at feeding time and another smaller peak at 400 to 700 h (Figure VI.2). Rumination followed a similar pattern with peaks in percentage of time spent ruminating occurring at 1100 to 1400 h and 0400 to 0700 h.

Treatment and period variations in activity

i. Treatment variations

Representative values of all activity measures are shown in Table VI.1 for selected periods of measurements during restricted and *ad libitum* feeding. Analyses of variance revealed significant treatment differences in standing duration both for the daily total and amount of time in the light phase for particular measurement periods. Group B spent approximately 30% greater time standing per day than group D in measurement period 3. Similarly, group B spent 25% to 30% greater time standing per day than both groups C and D during measurement period 4.

Although there was no significant difference in the total time standing per d for any of the groups in period 1 and 2, there was a significant difference in the time spent standing in the light portion of the day. In period 1 group D and in period 2 both groups C and D spent a significantly greater time standing during the light phase than group B. The ewes in group B similarly spent significantly greater time standing in the light phase than the ewes in groups C and D during measurement periods 4 and 5. In both cases, this was an increase of approximately 35%.

No significant differences related to imposed light treatments were observed for head or jaw movements for daily totals or proportion in light phase (number/min light), with the exception of up and down head movements being significantly greater for group B in period 5 (Table VI.1).

ii. Period differences

During restricted feeding, the ewes spent between 40 and 50% of the day standing. However during *ad libitum* feeding there was a significant decrease over time in daily standing time for all groups. Standing time decreased from an average daily total of 558 ± 96 min/day during the first 4 weeks of *ad libitum* feeding to 358 ± 39.3 min/day during the final 4 weeks. There was also a significant decrease in total jaw movements with time for all groups during the *ad libitum* feeding trial.

For the restricted feeding periods, there was a significant relationship between the hours of daylight experienced and the standing duration in light phase in relation to the amount of light exposure ($R^2=0.72$, $P=0.0005$). As shown in Figure VI.4, there was a linear decline in standing time per min of light with an increase in daily light exposure. No relationships were apparent between h of light and other activities or between MHp and various activities.

For the *ad libitum* feeding periods there was a significant relationship between MHp (M/kg$^{.75}$/d) and total number of jaw movements (R^2=0.66, P=0.00014) and MHp (M/kg$^{.75}$/d) and daily standing duration (R^2=0.32, P=0.02), with a linear decline in total jaw movements and standing duration with a decrease in MHp. There was also a significant relationship between liveweight and total standing duration (R^2=0.46, P=0.004), such that standing duration decreased with an increase in liveweight (Figure VI.4).

DISCUSSION

Photoperiodic influences were observed for standing activity, but there were no significant patterns in relation to light in the other activities measured. Differences in jaw movements were not expected for measurement periods 4 to 6, as there were found to be no treatment differences in the voluntary food intake or metabolic heat production of the ewes at these times (Chapter V). There were a limited number of measurements done during period 7 as there were health problems noted for some of the ewes at this time and this may account for a lack of differences during the final measurement period.

Daily Activity Pattern

A distinct daily activity pattern in standing and head movements was observed for all groups during the restricted feeding period. The initial peak in standing time and side to side head movements corresponds to the time of arrival of farm workers and the subsequent cleaning of the ewes cages during the week. The time of this peak also coincides with the time the lights came on in the rooms. Studies have found that when natural or artificial daily light-dark cycles are imposed on confined animals, they are most active around sunrise (or when the lights go on) and again around sunset (when the lights go off) (Curtis, 1981). This peak was present even on weekends when human activities were minimal, suggesting that the onset of daylight also contributed to the increase in activity.

The second peak, beginning one to two hours prior to feeding time, was in anticipation of feed with appetite being an important factor.

The ewes displayed a stereotyped restless behaviour involving the banging and chewing of their dishes and playing with the salt blocks in their dishes during this time. The performance of set patterns in the behaviour of sheep have been reported previously in relation to events which excite the animal such as feeding (Hecker, 1983). Done (1975) observed that patterns of stereotype behaviour not seen in newly introduced sheep were obvious in sheep that had been confined for about 6 months and very prominent in sheep confined for up to 2 years. The peak in standing or head movements resulted during eating. During restrict feeding, eating would usually last for 30-60 min. Following this there was an elevation in activity up until the approximate time the lights went off. This again supports findings of increases in activity at 'dusk'.

A similar daily pattern was observed for *ad libitum* feeding with a reduction in the intensity of the feeding peak (Figure V.2). Part of this pattern was likely a conditioned response from the previous restricted feeding period as appetite would no longer be a strong contributing factor.

Treatment Variations in Activity

Exposure of groups C and D to longer daylengths may have contributed to the 30% reduction in standing per day during measurement periods 3 and 4, in relation to group B in the reverse light situation. Support for the influence of amount of light exposure on standing time is provided by results of a recent study by Phillips and Schofield (1989), whereby natural daylength was extended by an additional 10 h of artificial light for dairy cows housed in winter. The cows in naturally short daylengths stood approximately 20% longer per day than the cows exposed to the artificially extended daylengths (Phillips and Schofield, 1989).

Photoperiodic influences were also evident for the time spent standing during the light portion of the day. For both the restrict and initial periods of *ad libitum* feeding, those sheep exposed to short daylengths spent 30 to 40% greater time standing during the light phase of the day. There was a linear decrease for standing duration (min/min light) with an increase in the amount of daily light exposure (Figure VI.4) for the restrict fed periods. However, this relationship was not evident for the *ad libitum* feeding trial as other factors shown to contribute to the daily standing activity of the sheep became prominent at this time. Toutain et al., (1977) found a significant difference in the time spent standing for sheep of different ages and body weights. Yearling sheep were found to spend the smallest time standing (191 min/15 h) followed by 4-6 year old fat sheep (294 min/15h) and then 4-6 year thin sheep (356 min/15h). In the present study, the sheep increased in weight during *ad libitum* feeding from a stabilized average weight of 58 kg to a final average weight of 94 kg. Standing time for this period was therefore found to be more closely related in a linear manner to the changes in liveweight than to h of light (Figure VI.4).

The general findings do not provide support for the theory of changes in activity contributing to the to the seasonal changes in metabolic heat production. During *ad libitum* feeding, MHp was closely correlated to food intake, as evidenced by the relationship MHp to jaw movements. The pattern of head movements were influenced primarily by feeding activities with no differences seen related to light treatments. This method of head movement measurement may not serve as the best measure of activity of the sheep and other areas need examination. Videotaping of activity has become more widely utilized and may be a more useful tool to examine and classify specific activities and their timing.

Activities such as standing have been shown to have an energy cost for sheep of 0.5 to 0.7 kJ/kg W/h (Toutain et al., 1977; Osuji, 1974). Based on a cost of standing of 0.5 kJ/kg W/h, the contribution of standing to daily total MHp was calculated and found to be only a small portion of the daily total MHp. The contribution was approximately 4.5 to 5.0 percent for restrict feeding and 1.5 to 2.0 percent for the *ad libitum* feeding trial. Variations in standing duration were not found to be a contributing factor to variations in metabolic heat production as increases in standing duration did not coincide with increases in MHp during restrict feed. In contrast, the reverse situation was evident although not significant, with a decrease in MHp (M/kg.75/d) coincident with an increase in standing duration (R^2-0.31, P-0.06).

It would appear that changes resulted in the energy expenditure of sheep during restricted feeding, which were not explained by the physical activity parameters examined. However, measurements taken were limited to the final 20 weeks of the restricted feeding trial. Toutain et al. (1977) suggested that the state of vigilance could have a significant effect on daily energy expenditure. Heat production was found to decrease by 10-20% in sheep when asleep compared to when awake (Toutain et al., 1977). The state of vigilance of the sheep in the various light environments may be a contributing factor to the variations observed in MHp.

The findings of this study could also support a hypothesis by Phillips and Schofield (1989) suggesting that other physiological mechanisms involving hormonal changes and shifts in reactions at the cellular level (substrate cycles), may account for changes in parameters such as energy metabolism that occur in relation to photoperiod. Changes in thyroid hormones, which are known to increase cellular enzymes and processes such as protein synthesis (Guyton, 1986), were found to coincide with changes observed in metabolic heat production in the present study and may therefore be the important factor influencing the changes in MHp.

Table VI.1 - Standing duration (min) and head movements, for daily totals (sum of 24 h values) and value in light phase based on minutes of light received during the 24 h measurement.

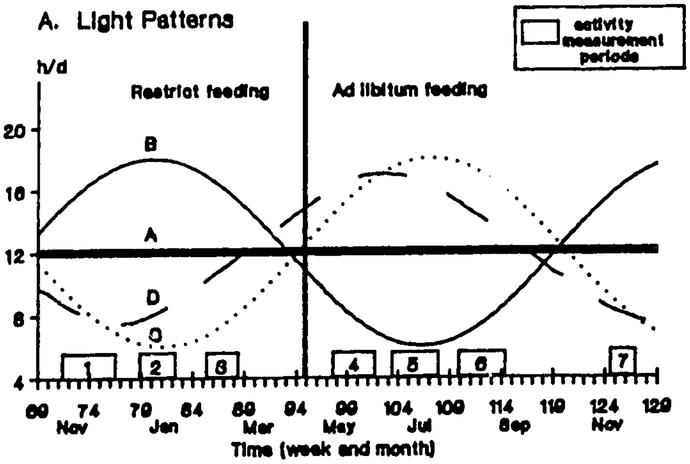
Activity	Group A	Group B	Group C	Group D
A. Measurement period 3 (restricted feeding)				
Standing				
total (min)	$604^{ac} \pm 11$	$727^{b} \pm 12$	$632^{bc} \pm 12$	$530^{a} \pm 12$
light*	$0.56^{a} \pm 0.02$	$0.58^{a} \pm 0.02$	$0.78^{b} \pm 0.02$	$0.55^{a} \pm 0.02$
Head movements				
Side to side				
total	$53323^{a} \pm 4739$	$47342^{a} \pm 3705$	$57473^{a} \pm 4433$	$58153^{a} \pm 4239$
light*	$48.3^{a} \pm 8.8$	$38.0^{a} \pm 6.9$	$58.7^{a} \pm 8.3$	$52.7^{a} \pm 7.9$
Up and down				
total	$4166^{a} \pm 1125$	$10616^{b} \pm 1125$	$6794^{ab} \pm 1289$	$6293^{ab} \pm 1233$
light*	$3.9^{a} \pm 2.3$	$8.8^{b} \pm 2.3$	$9.3^{ab} \pm 2.6$	$5.7^{ab} \pm 2.5$
B. Measurement period 5 (*ad libitum* feeding)				
Standing				
total (min)	$494^{a} \pm 27$	$499^{a} \pm 30$	$470^{a} \pm 35$	$348^{a} \pm 41$
light	$0.42^{ac} \pm 0.09$	$0.52^{c} \pm 0.12$	$0.37^{ab} \pm 0.04$	$0.29^{b} \pm 0.07$
Head movements				
Side to side				
total	$41332^{a} \pm 6115$	$51063^{a} \pm 7155$	$61440^{a} \pm 7834$	$54554^{a} \pm 9366$
light*	$27.8^{a} \pm 4.0$	$37.3^{a} \pm 4.7$	$36.9^{a} \pm 4.6$	$36.3^{a} \pm 5.8$
Up and down				
total	$8588^{a} \pm 683$	$13592^{b} \pm 670$	$10969^{a} \pm 1189$	$10053^{a} \pm 1039$
light*	$6.8^{a} \pm 0.7$	$12.2^{b} \pm 0.6$	$8.0^{a} \pm 1.1$	$8.1^{a} \pm 1.0$
Jaw movements				
total	$32118^{a} \pm 3363$	$30228^{a} \pm 3686$	$34109^{a} \pm 4414$	$40926^{a} \pm 4948$
light*	$25.8^{a} \pm 3.0$	$31.1^{a} \pm 3.3$	$25.9^{a} \pm 4.0$	$30.0^{a} \pm 4.4$

$^{a\ b\ c}$ means with different superscript in a row differ ($P<0.05$).
values are given as least square means ± standard error of the mean
* standing value expressed as min/min daylight, head and jaw movements expressed as no. of movements/min of daylight.

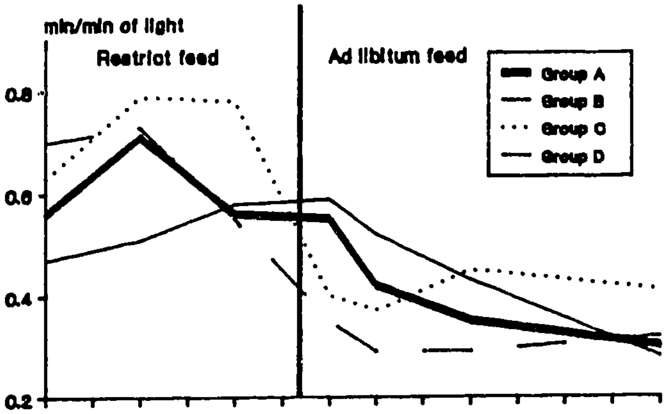
Group A, constant 12L:12D
Group B, artificial sinusoidal light pattern, reverse of natural light.
Group C, artificial sinusoidal light pattern, closely mimicking natural light.
(artficial summer and winter 'solstices' 18L:6D and 6L:18D, respectively).
Group D, natural light pattern, 53.5° N latitude.

Figure VI.1. Light patterns and least square means for standing duration of each group for each measurement period

A. Light Patterns



B. Time standing (min/min of light)



C. Total daily standing time

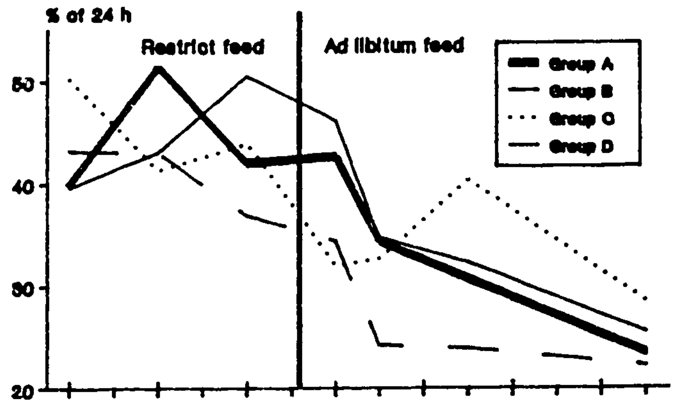
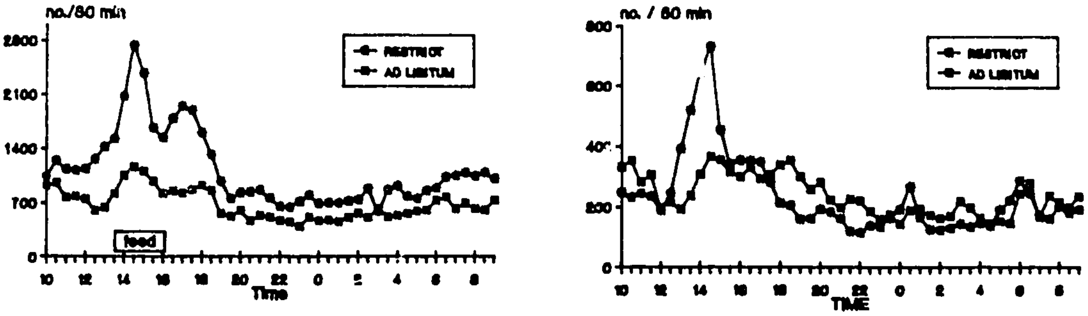


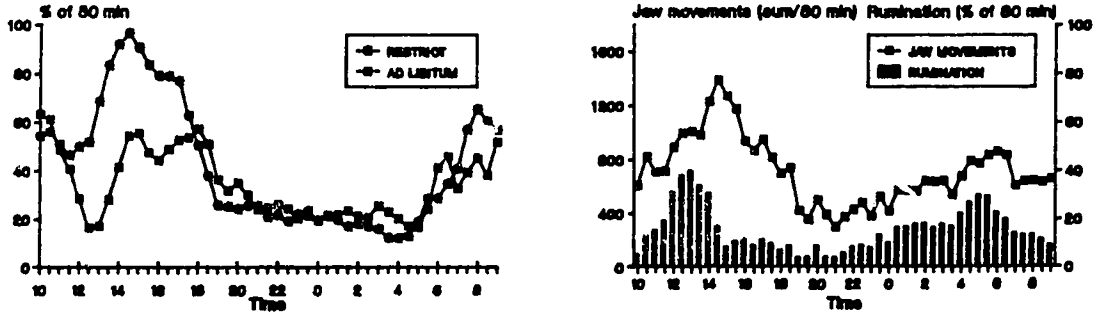
Figure VI.2. Daily activity patterns for restricted and ad libitum feeding trial

(* jaw movements and rumination only measured during ad libitum feeding)



A. Side to side head movements

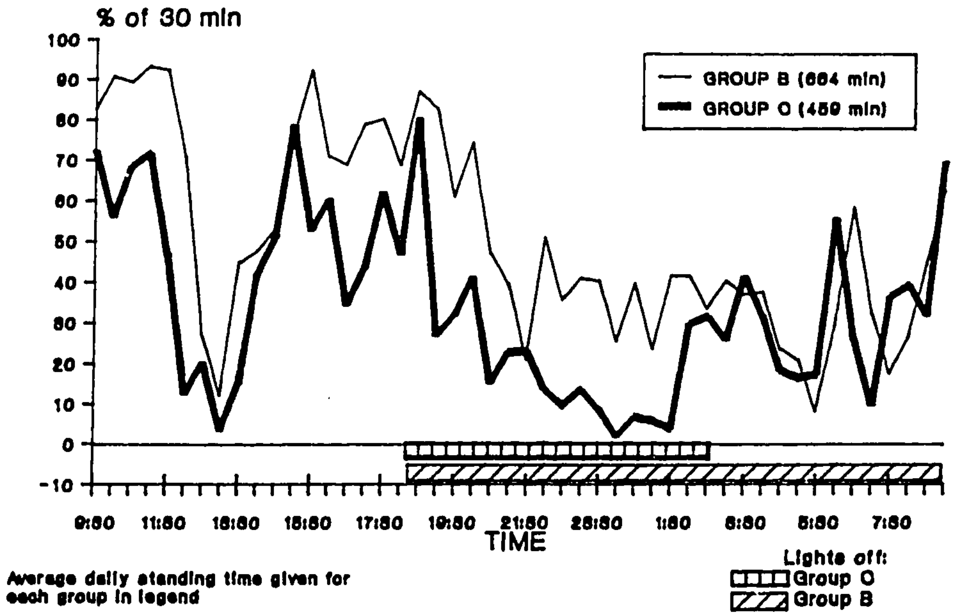
B. Up and down head movements



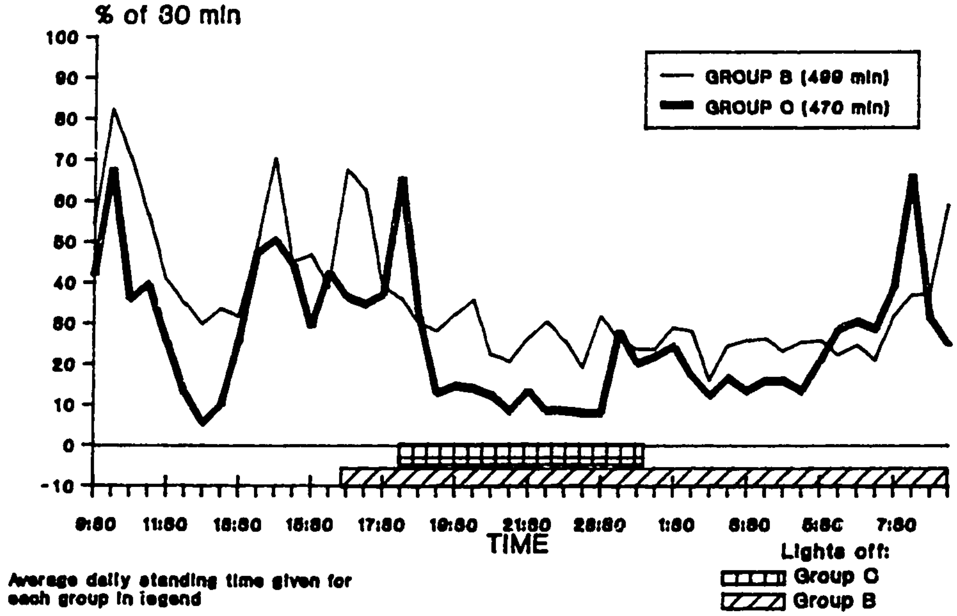
C. Daily standing pattern

D. Jaw movements and rumination time

Figure VI.3. Daily standing pattern for period 4 and 5

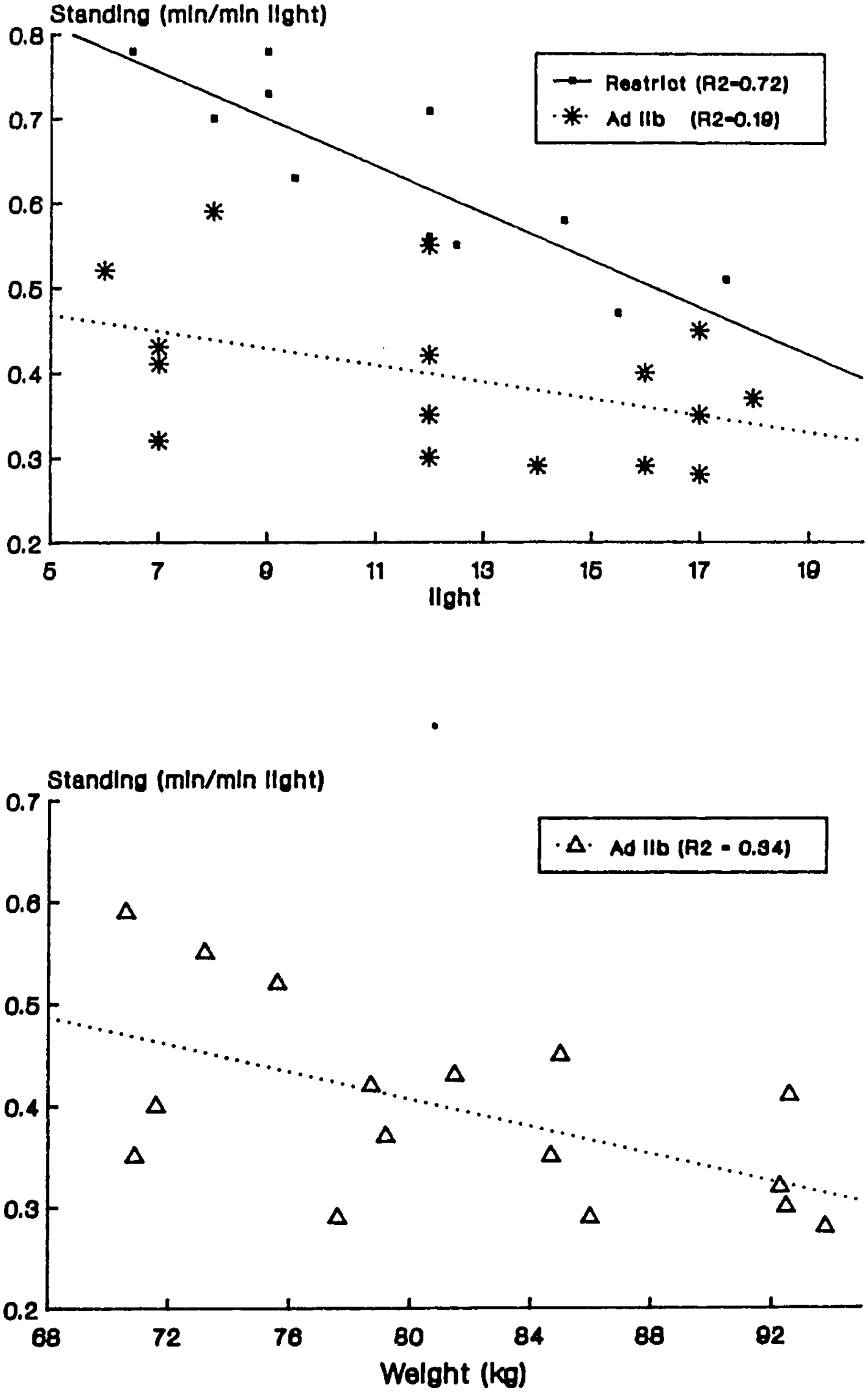

Period 4

Average daily standing time given for each group in legend


Period 5

Average daily standing time given for each group in legend

Figure VI.4. Observed values for daily standing duration in relation to (A) hours of daily light exposure and (B) liveweight and the calculated regression



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VII. GENERAL DISCUSSION

Photoperiod is one of the most consistent and best known seasonal predictors utilized by animals to ensure that physiological processes are in harmony with existing environmental conditions. The sheep is one example of an animal which is physiologically fine-tuned to its external environment via photoperiodic cues, as evidenced in its reproductive function (Yeates, 1949).

As mentioned, the mechanism by which light information is sensed in mammals occurs via the retina and a complex of neural pathways sent to the pineal gland. Melatonin released from the pineal gland is thought to act as the 'neuroendocrine transducer' converting the light and correlated neural information of the environment into an endocrine message available to all tissues (Cassone, 1990). How melatonin influences other endocrine responses varies between mammalian species (Kennaway, 1984). In terms of seasonal reproductive function, melatonin is often referred to being antigonadal in action (Vriend, 1983). However, this hypothesis has been derived mainly from animals which are long-day breeders (Kennaway, 1984). In animals which are short-day breeders such as domestic sheep, evidence has shown that melatonin serves both an inductive and inhibitory action on the reproductive axis and has been referred to as a timekeeping hormone (Karsch, 1986).

Distinct seasonal cycles in the energy metabolism and voluntary food intake of wild and domestic ungulates have been reported (Kay, 1985). However changes observed in metabolic heat production (MHp) have generally been attributed to the photoperiod induced changes in voluntary food intake. Although Blaxter and Boyne (1982) found a seasonal pattern in MHp independent of food intake, the mechanism by which this occurred was still undetermined.

The present study provided a highly controlled, comprehensive examination of factors influencing and controlling seasonal changes in MHp processes. A schematic of the parameters examined in the present study is shown in Figure VII.1, with the main focus of the study on the energy metabolism of the animal, as was indicated by MHp. Parameters known to influence MHp, including temperature, food intake and activity were maintained near constant allowing for the examination of influences related strictly to photoperiodic variations. This study serves to reconcile different responses observed in relation to temperature in the field situation versus a laboratory setting. The primary hypothesis of the study was that photoperiod was the main cue responsible for the seasonal metabolic pattern observed in ungulates (Silver et al., 1969; Renecker and Hudson, 1986), which then serves to stimulate appetite.

The initial part of the study (Chapter II), provided support for this hypothesis whereby seasonal variations in photoperiod, both artificial and natural, elicited a pattern in MHp of ewes with a constant near maintenance food intake. However, some of the ewes in constant light provided evidence of inherent patterns. In the second stage of the study (chapter III), it became evident that although photoperiod was the primary cue, hormonal changes in response to the light, were the mechanism responsible for changes in energy metabolism. Thyroid hormones (specifically total T3 and free T3 and T4 plasma concentrations) were most responsive serving to drive the metabolic response, as thyroid hormones are known to regulate basal metabolic rate through its influence on protein synthesis, cellular enzyme systems, mitochondria and the active transport of ions through cell membranes (van Hardeveld, 1986; Nunez, 1988). Thyroid patterns, also provided evidence to support the hypothesis linking the metabolic processes and reproductive axis (Chapter IV). The cessation of estrous cycles coincided closely with increased plasma levels of thyroid hormones and is in support of recent studies in which thyroidectomy resulted in disruption of the cessation of estrous (Nicholls et al., 1988).

The pineal gland has been shown to influence the neuroendocrine-thyroid axis in hamsters in an inhibitory manner similar to its anti-gonadal action (Vriend, 1983). Current findings lend support to anti-thyroidal activity in sheep whereby thyroid hormone levels were found to decrease at the time when the duration of melatonin secretion has been shown to increase with shortening daylengths (Karsch, 1986). This supports the hypothesis of a modulatory influence of the pineal gland on the neuro-endocrine-thyroid axes and the neuroendocrine-gonadal axes (Vriend, 1983), with decreasing daylength inhibiting thyroid activity but stimulating reproductive activity in the ewes.

The implications of the link between reproductive and metabolic function relate to the necessity to synchronize the timing of these processes as one is dependent on the other. Increases in metabolism coincide with the time of increased feed availability, thus enabling attainment of proper body condition necessary for reproduction and production of offspring or milk, with young born at a time of the year to allow the highest probability of survival. The findings of the present study provide evidence for an intricately coordinated and integrated system with thyroid hormones serving in a dual manner to regulate both the termination of one system and the initiation of another.

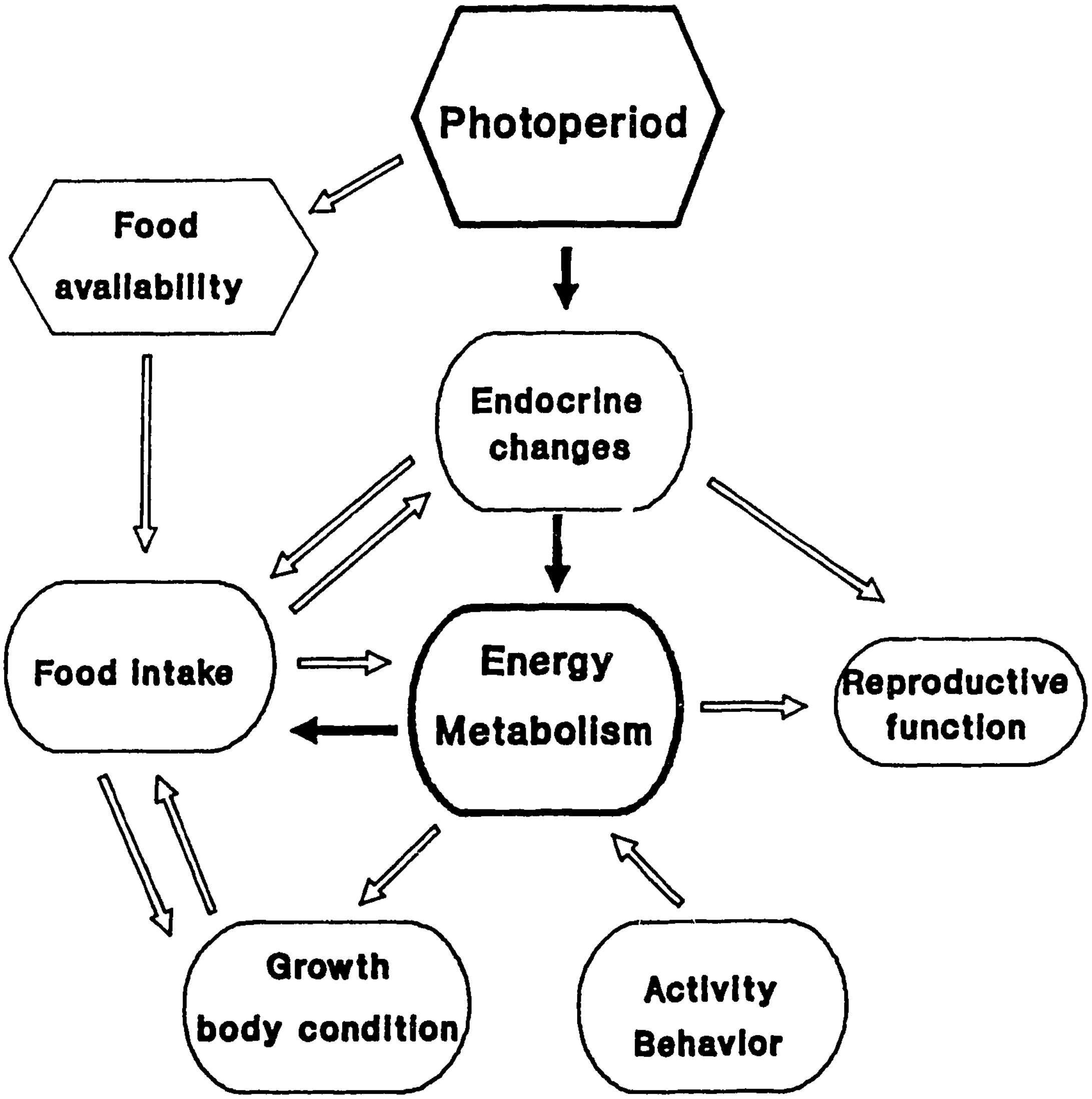
The utilization of exogenous thyroxine has been previously shown to stimulate food intake of sheep (Forbes, 1986). However, feed intake patterns of the ewes in the present study appeared to be regulated by 2 or 3 different driving forces (Chapter V). Feed intake was regulated initially by the inherent drive to achieve the genetically determined maximum body mass or composition (Blaxter et al., 1982, Young, 1987). Once attained, then the known photoperiodic modulation of intake (Simpson et al., 1984) became increasingly evident, with the group exposed to increasing daily light having the greatest intake. MHp was closely correlated with food intake, supporting previous evidence of food intake effects on MHp (Webster, 1983). Photoperiod serves to modulate the metabolic response, stimulating appetite at times of increased food availability in the natural environment. Similarly, the low MHp is advantageous coinciding with natural times of decreases in food availability, leaving more of a limited energy consumption for use in thermoregulation and requiring less tissue mobilization.

The light patterns and associated thyroid hormone patterns accounted for most of the MHp response at constant feed intake. Apparent visual differences in the ewes behaviour were not reflected in the measured activity parameters which were similar between groups with the exception of daily standing patterns (Chapter VI). Daily standing duration was greatest with exposure to decreasing daylengths although generally not significant but a significantly greater proportion of time was spent standing during the daylight period for those ewes exposed to short photoperiod.

In conclusion, the experimental findings supported the primary hypothesis that photoperiod serves to induce seasonal changes in energy metabolism, independent of food intake. In addition, the study also provided information as to the physiological mechanisms regulating metabolism, and is a step towards understanding the interaction of seasonally induced physiological changes.

Future studies should focus on interactive environmental influences such as seasonal photoperiod and temperature. Similar work has focused on the interactive effects of these parameters on reproductive response such that the observed rate at which short photoperiod induced gonadal atrophy in hamsters was found to be dependent on environmental temperature (Pévet, 1986). Also future research into the mechanisms responsible for the changes in MHp and reproduction and how these systems interact. To understand the contribution of particular factors individual analysis is necessary but the interaction of components is necessary to provide a more complete understanding of the whole functioning system in seasonally sensitive animals, enabling development of efficient and cost effective production systems.

Figure VII.1. General schematic of photoperiodic influence on physiological parameters



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APPENDIX

TABLE 1
Metabolic rate (watt) - water bath method

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7	72.1	65.7	68.5	73.7	92.8	68.6	67.3	72.0	65.7	66.6	73.4	70.8
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13												
09/28/87	14												
10/05/87	15												
10/12/87	16	73.1	67.6	85.3	87.9	79.8	67.6	76.3	78.5	76.8	77.2	79.8	69.0
10/19/87	17												
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21	88.0	66.7	74.5	75.0	80.6	79.1	76.5	72.7	82.6	85.6	75.2	86.3
11/23/87	22												
11/30/87	23												
12/07/87	24												
12/14/87	25	72.8	71.9	75.6	72.9	88.3	74.0	68.3	81.2	88.3	79.8	61.5	83.3
12/21/87	26												
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	76.2	72.1	[illegible]	64.4	77.1	77.4	55.9	66.5	[illegible]	73.8	60.3	70.4
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34												
02/22/88	35	70.3	80.9	69.6	77.9	80.8	72.8	55.8	63.4	68.9	67.3	58.9	73.7
02/29/88	36												
03/07/88	37												
03/14/88	38												
03/21/88	39	77.2	66.4	72.5	64.9	74.9	70.9	63.3	65.8	66.3	70.4	52.6	67.8
03/28/88	40												
04/04/88	41												
04/11/88	42												
04/18/88	43												
04/25/88	44	74.8	71.1	77.8	60.8	83.8	80.7	60.4	73.9	71.2	66.0	67.8	63.1
05/02/88	45												
05/09/88	46												
05/16/88	47	69.7	62.0	73.5	71.9	70.5	61.6	60.7	68.3	61.4	72.0	56.0	63.1
05/23/88	48												
05/30/88	49												
06/06/88	50												
06/13/88	51	61.4	61.9	66.5	61.4	80.4	67.2	70.9	70.7	72.3	69.7	68.8	68.8
06/20/88	52												
06/27/88	53												
07/04/88	54												
07/11/88	55												
07/18/88	56	66.6	70.9	76.5	78.2	77.7	73.7	61.9	66.5	66.1	76.7	68.8	70.8
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	74.0	64.2	69.8	62.6	80.0	72.4	70.9	64.9	75.7	76.7	67.8	71.0
08/22/88	61												
08/29/88	62												
09/05/88	63												
09/12/88	64	67.3	63.3	69.7	65.5	76.6	64.1	75.7	74.3	77.7	75.7	66.6	88.6
09/19/88	65												
09/26/88	66												
10/03/88	67												
10/10/88	68												
10/17/88	69	68.4	62.9	73.6	72.9	73.9	66.4	74.2	78.9	71.2	87.4	75.7	83.7
10/24/88	70												

TABLE 1
Metabolic rate (watt) - water bath method

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
10/31/88	71												
11/07/88	72	83.6	70.3	83.5	70.4	87.1	78.5	69.6	92.6	76.5	99.8	72.6	89.4
11/14/88	73												
11/21/88	74												
11/28/88	75	77.1	60.3	75.6	82.8	80.1	76.1	74.6	72.4	74.3	96.7	68.7	82.3
12/05/98	76												
12/12/88	77												
12/19/88	78	66.7	66.5	72.4	72.9	80.6	75.2	63.9	67.7	66.4	84.6	70.2	68.9
12/26/08	79												
01/02/89	80												
01/09/89	81												
01/16/89	82	73.5	67.8	80.0	80.9	98.7	80.5	72.9	75.6	66.7	89.8	68.4	75.5
01/23/89	83												
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87	71.4	73.0	77.6	79.0	88.8	75.8	68.5	73.8	68.6	82.5	73.6	74.4
02/27/89	88												
03/06/89	89												
03/13/89	90												
03/20/89	91	74.1	70.3	76.0	71.5	98.6	75.3	62.8	73.1	72.2	79.0	63.9	74.8
03/27/89	92												

TABLE 1
Metabolic rate (watt) - water bath method

		---GROUP C (artificial light)----						---------GROUP D (NATURAL)-------------					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7	70.3	73.3	78.3	62.9	70.4	73.2						
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13												
09/28/87	14												
10/05/87	15												
10/12/87	16	67.5	83.2	87.3	70.2	77.0	84.2	63.5	75.6	63.4	60.9	69.7	69.9
10/19/87	17												
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21	69.8	70.6	86.8	72.6	71.4	75.9	67.8	75.5	60.9	61.1	59.5	65.1
11/23/87	22												
11/30/87	23												
12/07/87	24												
12/14/87	25	66.3	63.4	70.8	74.1	72.0	65.9	59.6	67.7	59.7	66.5	63.8	68.9
12/21/87	26												
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	68.7	67.2	65.2	70.9	68.1	50.2	64.9	77.1	62.6	74.5	58.1	80.3
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34												
02/22/88	35	73.1	76.7	75.9	76.0	82.7	74.7	75.7	67.9	77.7	81.6	74.1	80.1
02/29/88	36												
03/07/88	37												
03/14/88	38												
03/21/88	39	74.2	75.3	75.5	78.3	79.4	64.9	77.7	72.5	78.0	92.8	78.3	76.8
03/28/88	40												
04/04/88	41												
04/11/88	42												
04/18/88	43												
04/25/88	44	76.4	80.5	77.3	76.9	89.6	79.0	86.6	81.6	80.3	77.3	71.1	80.0
05/02/88	45												
05/09/88	46												
05/16/88	47	73.2	75.9	68.6	80.8		67.6	87.9	75.1	75.5	62.4	72.3	68.7
05/23/88	48												
05/30/88	49												
06/06/88	50												
06/13/88	51	76.7	79.7	76.9	74.4	79.7	72.3	68.9	82.3	74.0	59.7	70.7	62.2
06/20/88	52												
06/27/88	53												
07/04/88	54												
07/11/88	55												
07/18/88	56	74.1	66.9	67.7	68.3	79.2		65.8	73.8	75.7	73.1	77.5	71.5
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	67.3	66.4	73.4	74.9	75.4		70.5	79.4	63.2	59.2	66.0	63.7
08/22/88	61												
08/29/88	62												
09/05/88	63												
09/12/88	64	61.9	66.6	66.3	65.5	73.2		63.3	68.7	65.8	63.0	62.5	73.2
09/19/88	65												
09/26/88	66												
10/03/88	67												
10/10/88	68												
10/17/88	69	67.	63.3	65.7	62.0			64.1	66.0	74.1	62.0	63.3	59.1
10/24/88	70												

TABLE 1
Metabolic rate (watt) - water bath method

		GROUP C (artificial light)						GROUP D (NATURAL)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
10/31/88	71												
11/07/88	72	66.4	63.0	69.0	67.9			57.5	66.2	75.6	67.5	71.1	70.0
11/14/88	73												
11/21/88	74												
11/28/88	75	64.0	64.4	67.9	73.3			59.0	73.8	70.4	68.0	61.1	72.0
12/05/88	76												
12/12/88	77												
12/19/88	78	65.0	65.1	64.4	63.3			65.6	64.5	58.0	67.7	65.7	61.9
12/26/88	79												
01/02/89	80												
01/09/89	81												
01/16/89	82	69.6	75.4	67.5	65.5			65.7	75.3	82.1	79.1	72.8	
01/23/89	83												
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87	75.3	85.8	68.0	69.9			81.0	72.4	106.4	79.1	83.2	
02/27/89	88												
03/06/89	89												
03/13/89	90												
03/20/89	91	79.6	82.0	75.8	87.6			73.8	82.6	101.1	75.7	93.3	
03/27/89	92												

TABLE 2
Live weight (kg)
restricted (week 1-92) and ad libitum (week 93-130) feeding periods

		GROUP A (12L:12D)						GROUP B (artificial light)					
	Sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
06/29/87	1	46.0	35.0	51.0	48.0	42.0		36.0	47.0	50.0	41.0	50.0	46.0
07/06/87	2												
07/13/87	3	45.0	36.0	48.0	49.0	42.0	36.0	37.0	44.0	47.0	41.0	48.0	45.0
07/20/87	4												
07/27/87	5	44.0	35.0	48.0	49.0	42.0	34.0	37.0	44.0	46.0	42.0	49.0	45.0
08/03/87	6												
08/10/87	7	48.0	37.5	50.0	50.5	43.5	37.0	40.0	48.0	49.0	44.5	52.0	46.5
08/17/87	8												
08/24/87	9	48.0	40.0	55.0	52.0	47.0	39.0	41.0	49.0	49.0	48.0	50.0	50.0
08/31/87	10												
09/07/87	11	50.0	44.0	56.0	52.0	49.0	41.0	42.0	50.0	52.0	48.0	52.0	50.0
09/14/87	12												
09/21/87	13	49.0	43.0	55.0	52.0	48.0	41.5	42.0	49.0	50.0	48.0	53.0	50.0
09/28/87	14												
10/05/87	15	51.0	44.0	58.0	55.0	51.0	44.0	45.0	52.0	55.0	51.0	54.0	53.0
10/12/87	16												
10/19/87	17	53.0	47.0	58.0	56.0	52.0	46.0	46.0	53.0	53.0	50.0	57.0	54.0
10/26/87	18												
11/02/87	19	52.0	45.0	56.0	54.0	51.0	46.0	46.0	51.0	52.0	50.0	56.0	54.0
11/09/87	20												
11/16/87	21	53.0	46.5	59.0	56.0	53.0	47.0	47.0	51.0	54.0	52.0	55.0	56.0
11/23/87	22												
11/30/87	23	54.0	49.0	60.0	58.0	54.0	48.0	49.0	53.0	56.0	54.0	57.0	55.0
12/07/87	24												
12/14/87	25	54.0	49.0	61.0	59.0	54.0	48.0	50.0	55.0	56.0	55.0	59.0	50.0
12/21/87	26												
12/28/87	27	55.0	50.0	62.0	58.0	55.0	48.0	50.0	55.0	56.0	55.0	58.0	50.0
01/04/88	28	54.0	48.0	60.0	57.0	53.0	49.0	48.0	54.0	54.0	54.0	56.0	44.0
01/11/88	29												
01/18/88	30	56.0	51.0	62.0	58.0	55.0	50.0	50.0	57.0	56.0	56.0	59.0	46.0
01/25/88	31												
02/01/88	32	56.0	52.0	62.0	58.0	57.0	52.0	49.0	56.0	56.0	56.0	58.0	48.0
02/08/88	33												
02/15/88	34	59.0	54.0	66.0	62.0	58.0	52.0	54.0	58.0	60.0	58.0	60.0	52.0
02/22/88	35												
02/29/88	36	56.0	52.0	63.0	60.0	57.0	52.0	51.0	56.0	58.0	57.0	59.0	50.0
03/07/88	37												
03/14/88	38	58.0	52.0	63.0	61.0	58.0	52.0	52.0	58.0	57.0	57.0	60.0	50.0
03/21/88	39												
03/28/88	40	59.0	55.0	65.0	63.0	60.0	56.0	52.0	58.0	58.0	58.0	61.0	52.0
04/04/88	41												
04/11/88	42	59.0	55.0	67.0	63.0	61.0	57.0	53.0	59.0	[illegible]	58.0	62.0	53.0
04/18/88	43	58.0	53.0	64.0	61.0	59.0	55.0	52.0	57.0	[illegible]	59.0	61.0	51.0
04/25/88	44	58.0	52.0	62.0	60.0	60.0	54.0	51.0	58.0	57.0	59.0	61.0	51.0
05/02/88	45												
05/09/88	46	59.0	52.0	63.0	60.0	61.0	55.0	51.0	59.0	60.0	59.0	61.0	52.0
05/16/88	47												
05/23/88	48	58.0	52.0	65.0	62.0	81.0	56.0	53.0	59.0	60.0	60.0	62.0	53.0
05/30/88	49												
06/06/88	50	60.0	51.0	66.0	64.0	62.0	56.0	54.0	60.0	60.0	60.0	64.0	53.0
06/13/88	51												
06/20/88	52	60.0	51.0	65.0	64.0	62.0	59.0	54.0	58.0	58.0	60.0	62.0	52.0
06/27/88	53												
07/04/88	54	60.0	52.0	65.0	64.0	61.0	58.0	55.0	58.0	60.0	60.0	62.0	53.0
07/11/88	55												
07/18/88	56	60.0	53.0	66.0	66.0	62.0	58.0	54.0	58.0	59.0	60.0	62.0	55.0
07/25/88	57												
08/01/88	58	60.0	53.0	66.0	65.0	63.0	58.0	54.0	59.0	58.0	60.0	63.0	56.0
08/08/88	59												
08/15/88	60	60.0	53.0	64.0	65.0	62.0	60.0	55.0	60.0	58.0	60.0	64.0	56.0
08/22/83	61												
08/29/88	62	60.0	53.0	68.0	66.0	63.0	59.0	56.0	60.0	60.0	61.0	66.0	57.0
09/05/88	63												
09/12/88	64	61.0	56.0	67.0	66.0	64.0	60.0	55.0	60.0	60.0	61.0	64.0	55.0
09/19/88	65												
09/26/88	66	62.0	56.0	68.0	66.0	65.0	60.0	55.0	60.0	60.0	61.0	64.0	55.0
10/03/88	67												
10/10/88	68	61.0	56.0	66.0	66.0	63.0	61.0	56.0	60.0	60.0	60.0	64.0	58.0

TABLE 2
Live weight (kg)
restricted (week 1-92) and ad libitum (week 93-130) feeding periods

		--------GROUP A (12L:12D)----------						----GROUP B (artificial light)-----					
	Sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
10/17/88	69												
10/24/88	70	61.0	56.0	66.0	66.0	63.0	61.0	56.0	60.0	60.0	61.0	65.0	56.0
10/31/88	71												
11/07/88	72	62.0	54.0	67.0	66.0	64.0	62.0	55 0	62.0	61.0	62.0	66.0	55.0
11/14/88	73												
11/21/88	74	62.0	54.0	66.0	67.0	64.0	62.0	54.0	62.0	61.0	62.0	62.0	58.0
11/28/88	75												
12/05/88	76	62.0	54.0	67.0	68.0	65.0	63.0	55.0	62.0	61.0	62.0	64.0	58.0
12/12/88	77												
12/19/88	78	62.0	56.0	68.0	68.0	66.0	63.0	56.0	62.0	61.0	62.0	63.0	59.0
12/26/88	79												
01/02/89	80	59.0	52.0	65.0	64.0	62.0	59.0	53.0	59.0	58.0	60.0	61.0	56.0
01/09/89	81												
01/16/89	82	60.0	54.0	66.0	65.0	64.0	60.0	54.0	60.0	60.0	62.0	58.0	57.0
01/23/89	83												
01/30/89	84	62.0	55.0	66.0	66.0	65.0	63.0	55.0	63.0	58.0	61.0	61.0	58.0
02/06/89	85												
02/13/89	86	62.0	55.0	65.0	67.0	64.0	64.0	55.0	61.0	59.0	63.0	61.0	58.0
02/20/89	87												
02/27/89	88	63.0	54.0	66.0	66.0	66.0	63.0	56.0	61.0	60.0	63.0	62.0	60.0
03/06/89	89												
03/13/89	90	62.0	54.0	66.0	68.0	65.0	61.0	55.0	59.0	58.0	60.0	60.0	59.0
03/20/89	91												
03/27/89	92	62.0	54.0	65.0	68.0	66.0	62.0	56.0	60.0	60.0	62.0	62.0	56.0
04/03/89	93												
04/10/89	94												
04/17/89	95	61.0	55.0	65.0	67.0	63.0	62.0	55.0	59.0	58.0	61.0	62.0	58.0
04/24/89	96	65.0	60.0	67.0	70.0	67.0	66.0	59.0	64.0	62.0	67.0	64.0	60.0
05/01/89	97	67.0	61.0	70.0	74.0	71.0	68.0	61.0	66.0	66.0	68.0	69.0	64.0
05/08/89	98	70.0	62.0	73.0	77.0	75.0	73.0	66.0	70.0	70.0	69.0	73.0	68.0
05/15/89	99	72.0	62.0	75.0	78.0	74.0	72.0	65.0	77.0	72.0	70.0	72.0	69.0
05/22/89	100	73.0	62.0	76.0	78.0	75.0	73.0	62.0		70.0	68.0	72.0	70.0
05/29/89	101	76.0	68.0	80.0	81.0	80.0	72.0	70.0		75.0	73.0	78.0	74.0
06/05/89	102	76.0	69.0	82.0	80.0	81.0	72.0	72.0		75.0	70.0	78.0	75.0
06/12/89	103	76.0	68.0	82.0	80.0	80.0	78.0	76.0		78.0	72.0	78.0	76.0
06/19/89	104	79.0	70.0	85.0	82.0	81.0	80.0	72.0		78.0	70.0	80.0	76.0
06/26/89	105	82.0	72.0	86.0	83.0	81.0	84.0	74.0		80.0	72.0	81.0	79.0
07/03/89	106	82.0	72.0	86.0	83.0	86.0	84.0	79.0		81.0	73.0	80.0	79.0
07/10/89	107	82.0	74.0	88.0	80.0	86.0	85.0	78.0		80.0	74.0	82.0	80.0
07/17/89	108	84.0	73.0	91.0	86.0	86.0	88.0	79.0		85.0	75.0	81.0	81.0
07/24/89	109	84.0	74.0	91.0	86.0	86.0	89.0	79.0		84.0	76.0	83.0	80.0
07/31/89	110	84.0	74.5	92.0	86.0	86.0	90.0	80.0		84.0	77.0	81.0	83.0
08/07/89	111	85.0	74.0	93.0	88.0	83.5	90.5	82.0		88.0	79.0	84.0	85.0
08/14/89	112	84.0	74.5	94.0	87.5	83.0	88.5	82.5		87.5	78.5	87.0	85.0
08/21/89	113	84.0	74.0	95.5	89.5	88.0	88.5	82.0		88.0	77.5	86.0	86.0
08/28/89	114	86.0	76.0	96.0	90.0	90.0	90.0	82.0		91.0	79.0	89.0	88.0
09/04/89	115	86.0	74.0	97.0	86.0	90.0	90.0	82.0		91.0	78.0	89.0	88.0
09/11/89	116	84.0	74.0	98.0	90.0	90.0	92.0	84.0		93.0	78.0	91.0	90.0
09/18/89	117	84.0	68.0	96.0	90.0	92.0	90.0	84.0		94.0	78.0	90.0	91.0
09/25/89	118	83.0	67.0	96.0	90.0	88.0	88.0	85.0		92.0	78.0	89.0	91.0
10/02/39	119	80.0	68.0	97.0	92.0	92.0	91.0	86.0		94.0	80.0	92.0	94.0
10/09/89	120	80.0	72.0	96.0	94.0	92.0	90.0	87.0		95.0	80.0	92.0	95.0
10/16/89	121	81.0	72.0	98.0	98.0	94.0	92.0	88.0		96.0	82.0	94.0	96.0
10/23/89	122	82.0	68.0	97.0	96.0	93.0	93.0	84.0		96.0	82.0	90.0	96.0
10/30/89	123	82.0	71.0	98.0	96.0	96.0	93.0	86.0		98.0	82.0	94.0	100.0
11/06/89	124	82.0	71.0	100.0	96.0	96.0	94.0	88.0		94.0	82.0	95.0	101.0
11/13/89	125	86.0	71.0	98.0	96.0	97.0	94.0	89.0		98.0	82.0	93.0	100.0
11/20/89	126	88.0	72.0	100.0	[illegible]	98.0	92.0	90.0		97.0	83.0	93.0	100.0
11/27/89	127	88.0	74.0	101.0	97.0	98.0	92.0	90.0		100.0	84.0	94.0	102.0
12/04/89	128	90.0	75.0	100.0	98.00	100.0	89.0	91.0		100.0	77.0	92.0	104.0
12/11/89	129	88.0	75.0	101.0	100.0	98.0	90.0	92.0		102.0	76.0	88.0	108.0
12/18/89	130	91.0	76.0	102.0	100.0	99.0	93.0	92.0		102.0	80.0		108.0

TABLE 2
Live weight (kg)
restricted (week 1-92) and ad libitum (week 93-130) feeding periods

		GROUP C (artificial light						GROUP D (NATURAL)					
	Sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
06/29/87	1	36.0	43.0	38.0	38.0	42.0	43.0						
07/06/87	2												
07/13/87	3	37.0	44.0	40.0	39.0	42.0	43.0						
07/20/87	4												
07/27/87	5	37.0	44.0	40.0	39.0	42.0	43.0						
08/03/87	6												
08/10/87	7	41.0	45.0	42.5	42.0	44.0	45.5						
08/17/87	8												
08/24/87	9	41.0	46.0	44.0	44.0	47.0	49.0						
08/31/87	10												
09/07/87	11	44.0	48.0	45.0	45.0	47.0	51.0						
09/14/87	12												
09/21/87	13	42.0	47.0	45.5	44.5	46.5	50.0	44.0	43.0	35.0	40.0	41.0	37.0
09/28/87	14												
10/05/87	15	45.0	49.0	48.0	47.0	49.0	52.0	46.0	46.0	38.0	41.0	42.0	39.0
10/12/87	16												
10/19/87	17	48.0	50.0	49.0	49.0	50.0	54.0	47.0	47.0	39.0	40.0	41.0	39.0
10/26/87	18												
11/02/87	19	45.0	48.0	48.0	47.0	48.0	52.0	46.0	46.0	37.0	38.0	41.0	38.0
11/09/87	20												
11/16/87	21	47.0	49.0	49.0	51.0	50.0	54.0	48.0	48.0	40.0	42.0	43.0	38.0
11/23/87	22												
11/30/87	23	48.0	52.0	50.0	51.0	50.0	54.0	48.0	49.0	40.0	42.0	42.0	40.0
12/07/87	24												
12/14/87	25	48.0	51.0	52.0	53.0	50.0	56.0	48.0	51.0	41.0	42.0	43.0	42.0
12/21/87	26												
12/28/87	27	48.0	54.0	52.0	52.0	51.0	58.0	49.0	50.0	42.0	42.0	43.0	42.0
01/04/88	28	47.0	49.0	49.0	50.0	49.0	54.0	48.0	49.0	40.0	42.0	41.0	41.0
01/11/88	29												
01/18/88	30	49.0	52.0	50.0	53.0	51.0	56.0	49.0	51.0	42.0	44.0	46.0	43.0
01/25/88	31												
02/01/88	32	50.0	53.0	52.0	54.0	50.0	56.0	49.0	52.0	45.0	45.0	46.0	45.0
02/08/88	33												
02/15/88	34	52.0	57.0	54.0	55.0	54.0	60.0	52.0	52.0	47.0	46.0	48.0	47.0
02/22/88	35												
02/29/88	36	51.0	52.0	54.0	53.0	53.0	57.0	51.0	53.0	46.0	46.0	48.0	45.0
03/07/88	37												
03/14/88	38	52.0	57.0	56.0	57.0	52.0	60.0	53.0	54.0	48.0	51.0	50.0	47.0
03/21/88	39												
03/28/88	40	52.0	56.0	56.0	56.0	56.0	59.0	55.0	55.0	50.0	51.0	50.0	50.0
04/04/88	41												
04/11/88	42	56.0	57.0	58.0	58.0	56.0	62.0	56.0	56.0	49.0	51.0	50.0	48.0
04/18/88	43	55.0	56.0	58.0	58.0	55.0	62.0	53.0	53.0	48.0	49.0	47.0	46.0
04/25/88	44	54.0	56.0	57.0	58.0	54.0	61.0	54.0	54.0	48.0	50.0	47.0	45.0
05/02/88	45												
05/09/88	46	56.0	56.0	58.0	56.0	55.0	62.0	54.0	53.0	48.0	50.0	48.0	45.0
05/16/88	47												
05/23/88	48	56.0	56.0	56.0	56.0	56.0	62.0	55.0	54.0	48.0	50.0	47.0	46.0
05/30/88	49												
06/06/88	50	57.0	57.0	56.0	59.0	58.0	63.0	56.0	55.0	49.0	50.0	49.0	47.0
06/13/88	51												
06/20/88	52	56.0	58.0	56.0	58.0	59.0	62.0	54.0	55.0	49.0	52.0	50.0	48.0
06/27/88	53												
07/04/88	54	56.0	58.0	58.0	59.0	60.0		56.0	54.0	50.0	52.0	49.0	49.0
07/11/88	55												
07/18/88	56	57.0	58.0	58.0	56.0	56.0		57.0	54.0	49.0	52.0	49.0	50.0
07/25/88	57												
08/01/88	58	58.0	58.0	57.0	57.0	56.0		58.0	55.0	50.0	52.0	50.0	48.0
08/08/88	59												
08/15/88	60	57.0	58.0	58.0	57.0	56.0		57.0	56.0	50.0	52.0	50.0	48.0
08/22/88	61												
08/29/88	62	56.0	57.0	57.0	58.0	56.0		57.0	55.0	51.0	53.0	50.0	48.0
09/05/88	63												
09/12/88	64	57.0	58.0	60.0	58.0	56.0		58.0	55.0	53.0	55.0	51.0	48.0
09/19/88	65												
09/26/88	66	58.0	58.0	60.0	58.0			60.0	55.0	54.0	55.0	53.0	50.0
10/03/88	67												
10/10/88	68	56.0	57.0	61.0	56.0			58.0	56.0	54.0	54.0	50.0	49.0

TABLE 2
Live weight (kg)
restricted (week 1-92) and ad libitum (week 93-130) feeding periods

		GROUP C (artificial light						GROUP D (NATURAL)					
	Sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
10/17/88	69												
10/24/88	70	57.0	57.0	61.0	57.0			57.0	56.0	53.0	54.0	49.0	48.0
10/31/88	71												
11/07/88	72	58.0	58.0	61.0	58.0			59.0	58.0	54.0	55.0	50.0	51.0
11/14/88	73												
11/21/88	74	59.0	59.0	60.0	60.0			58.0	59.0	55.0	55.0	52.0	50.0
11/28/88	75												
12/05/88	76	60.0	58.0	60.0	60.0			59.0	58.0	55.0	57.0	52.0	50.0
12/12/88	77												
12/19/88	78	58.0	60.0	60.0	60.0			60.0	58.0	57.0	58.0	55.0	50.0
12/26/88	79												
01/02/89	80	56.0	56.0	59.0	56.0			59.0	57.0	54.0	56.0	53.0	
01/09/89	81												
01/16/89	82	57.0	57.0	60.0	59.0			58.0	57.0	54.0	56.0	53.0	
01/23/89	83												
01/30/89	84	56.0	58.0	61.0	60.0			59.0	58.0	56.0	57.0	55.0	
02/06/89	85												
02/13/89	86	58.0	59.0	62.0	60.0			60.0	59.0	56.0	58.0	54.0	
02/20/89	87												
02/27/89	88	59.0	60.0	62.0	60.0			61.0	60.0	56.0	59.0	56.0	
03/06/89	89												
03/13/89	90	58.0	60.0	62.0	59.0			59.0	58.0	56.0	59.0	55.0	
03/20/89	91												
03/27/89	92	58.0	60.0	62.0	59.0			60.0	58.0	57.0	60.0	54.0	
04/03/89	93												
04/10/89	94												
04/17/89	95	58.0	58.0	62.0	58.0			58.0	57.0	56.0	59.0	51.0	
04/24/89	96	62.0	62.0	66.0	62.0			62.0	62.0	60.0	63.0		
05/01/89	97	66.0	68.0	70.0	68.0			68.0	67.0	65.0	67.0		
05/08/89	98	69.0	66.0	71.0	72.0			70.0	68.0	62.0	71.0		
05/15/89	99	70.0	67.0	73.0	72.0			72.0	71.0	65.0	73.0		
05/22/89	100	70.0	67.0	78.0	73.0			73.0	71.0	66.0	74.0		
05/29/89	101	76.0	70.0	78.0	74.0			76.0	74.0	70.0	78.0		
06/05/89	102	74.0	79.0	78.0	76.0			77.0	75.0	68.0	80.0		
06/12/89	103	77.0	80.0	78.0	82.0			77.0	74.0	75.0	81.0		
06/19/89	104	78.0	79.0	82.0	80.0			79.0	75.0	75.0	81.0		
06/26/89	105	78.0	80.0	84.0	82.0			82.0	76.0	82.0	85.0		
07/03/89	106	80.0	81.0	84.0	83.0			83.0	77.0	83.0	86.0		
07/10/89	107	80.0	82.0	86.0	86.0			84.0	78.0	82.0	87.0		
07/17/89	108	80.0	84.0	85.0	84.0			86.0	80.0	85.0	87.0		
07/24/89	109	81.0	80.0	86.0	86.0			86.0	80.0	84.0	82.0		
07/31/89	110	83.0	83.0	87.5	88.0			88.5	82.5	87.0	89.5		
08/07/89	111	84.5	86.0	88.0	89.5			90.0	82.0	87.5	92.5		
08/14/89	112	81.5	84.5	88.0	91.5			91.5	83.5	88.0	92.0		
08/21/89	113	85.0	87.0	90.0	93.0			92.0	84.0	89.0	92.0		
08/28/89	114	85.0	90.0	90.0	93.0			92.0	83.0	90.0	92.0		
09/04/89	115	86.0	90.0	90.0	93.0			92.0	83.0	90.0	92.0		
09/11/89	116	86.0	88.0	90.0	94.0			93.0	84.0	91.0	92.0		
09/18/89	117	84.0	88.0	88.0	95.0			93.0	86.0	88.0	92.0		
09/25/89	118	84.0	88.0	88.0	92.0			94.0	84.0	89.0	91.0		
10/02/89	119	86.0	92.0	90.0	94.0			96.0	86.0	91.0	93.0		
10/09/89	120	86.0	92.0	90.0	96.0			95.0	86.0	92.0	94.0		
10/16/89	121	88.0	94.0	90.0	98.0			96.0	86.0	92.0	93.0		
10/23/89	122	88.0	94.0	90.0	96.0			96.0	86.0	89.0	92.0		
10/30/89	123	89.0	94.0	91.0	99.0			97.0	86.0	92.0	95.0		
11/06/89	124	81.0	94.0	90.0	98.0			98.0	87.0	92.0	95.0		
11/13/89	125	85.0	96.0	92.0	100.0			98.0	84.0	93.0	95.0		
11/20/89	126	86.0	96.0	94.0	98.0			100.0	88.0	94.0	96.0		
11/27/89	127	88.0	96.0	90.0	98.0			98.0	86.0	90.0	94.0		
12/04/89	128	85.0	94.0		100.0			98.0	84.0	92.0	96.0		
12/11/89	129	88.0	92.0		98.0			96.0	86.0	90.0	97.0		
12/18/89	130	86.0			98.0			98.0	83.0	91.0	97.0		

TABLE 3
Wool Weight (gm)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	Sheep	48	49	74	85	188	239	20	39	47	81	93	246
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13												
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17	1254	1315	1162	1263	1487	1049	1378	1328	1404	851	1330	1180
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21												
11/23/87	22												
11/30/87	23												
12/07/87	24												
12/14/87	25												
12/21/87	26	615	690	625	750	790	690	470	480	590	465	485	500
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30												
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34	650	640	670	680	740	690	550	590	590	540	560	350
02/22/88	35												
02/29/88	36												
03/07/88	37												
03/14/88	38												
03/21/88	39												
03/28/88	40												
04/04/88	41												
04/11/88	42	730	620	740	740	840	760	550	680	635	620	630	350
04/18/88	43												
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47												
05/23/88	48												
05/30/88	49												
06/06/88	50												
06/13/88	51												
06/20/88	52												
06/27/88	53												
07/04/88	54												
07/11/88	55												
07/18/88	56	1040	940	1140	1160	1250	1200		900	1040	1190		450
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60												
08/22/88	61												
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65												
09/26/88	66	775	820	780	805	830	880	620	640	740	690	690	340
10/03/88	67												
10/10/88	68												

TABLE 3
Wool Weight (gm)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	Sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
10/17/88	69												
10/24/88	70												
10/31/88	71												
11/07/88	72												
11/14/88	73												
11/21/88	74												
11/28/88	75												
12/05/88	76												
12/12/88	77												
12/19/88	78	850	780	870	970	960	930	610	740	760	610	630	390
12/26/88	79												
01/02/89	80												
01/09/89	81												
01/16/89	82												
01/23/89	83												
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87												
02/27/89	88												
03/06/89	89												
03/13/89	90												
03/20/89	91												
03/27/89	92												
04/03/89	93	910	880	950	1050	1000	930	960	1150	1050	840	970	655
04/10/89	94												
04/17/89	95												
04/24/89	96												
05/01/89	97												
05/08/89	98												
05/15/89	99												
05/22/89	100												
05/29/89	101												
06/05/89	102												
06/12/89	103	1010	950	1000	1050	1180	1100	880		1030	930	1080	600
06/19/89	104												
06/26/89	105												
07/03/89	106												
07/10/89	107												
07/17/89	108												
07/24/89	109												
07/31/89	110												
08/07/89	111												
08/14/89	112												
08/21/89	113												
08/28/89	114												
09/04/89	115												
09/11/89	116												
09/18/89	117	1575	1575	1275	1700	1900	1850	1175		1600	1425	1275	1325
09/25/89	118												
10/02/89	119												
10/09/89	120												
10/16/89	121												
10/23/89	122												
10/30/89	123												
11/06/89	124												
11/13/89	125												
11/20/89	126												
11/27/89	127												
12/04/89	128												
12/11/89	129												
12/18/89	130	1300	1200	1500	1600	1850	1550	1100		1400	1300		1300
12/25/89	131												

TABLE 3
Wool Weight (gm)

		GROUP C (artificial light)						GROUP D (NATURAL)					
	Sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13												
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17	877	1446	1232	1115	1343	1352	368	422	428	342	347	377
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21												
11/23/87	22												
11/30/87	23												
12/07/87	24												
12/14/87	25												
12/21/87	26	520	780	635	635	670	670	470	500	530	350	380	500
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30												
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34	400	610	540	560	570	570	310	450	440	400	340	460
02/22/88	35												
02/29/88	36												
03/07/88	37												
03/14/88	38												
03/21/88	39												
03/28/88	40												
04/04/88	41												
04/11/88	42	470	810	570	660	580	615	480	590	510	520	490	530
04/18/88	43												
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47												
05/23/88	48												
05/30/88	49												
06/06/88	50												
06/13/88	51												
06/20/88	52												
06/27/88	53												
07/04/88	54												
07/11/88	55												
07/18/88	56	770	960	850	960	990							
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60												
08/22/88	61												
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65												
09/26/88	66	740	880	700	860	760		790	710	780	580	670	660
10/03/88	67												
10/10/88	68												

TABLE 3
Wool Weight (gm)

		GROUP C (artificial light)						GROUP D (NATURAL)					
	Sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
10/17/88	69												
10/24/88	70												
10/31/88	71												
11/07/88	72												
11/14/88	73												
11/21/88	74												
11/28/88	75												
12/05/88	76												
12/12/88	77												
12/19/88	78	670	910	840	870			600	650	670	600	550	
12/26/88	79												
01/02/89	80												
01/09/89	81												
01/16/89	82												
01/23/89	83												
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87												
02/27/89	88												
03/06/89	89												
03/13/89	90												
03/20/89	91												
03/27/89	92												
04/03/89	93	550	970	700	880			550	650	730	600	550	
04/10/89	94												
04/17/89	95												
04/24/89	96												
05/01/89	97												
05/08/89	98												
05/15/89	99												
05/22/89	100												
05/29/89	101												
06/05/89	102												
06/12/89	103	720	1010	780	860			740	770	920	840		
06/19/89	104												
06/26/89	105												
07/03/89	106												
07/10/89	107												
07/17/89	108												
07/24/89	109												
07/31/89	110												
08/07/89	111												
08/14/89	112												
08/21/89	113												
08/28/89	114												
09/04/89	115												
09/11/89	116												
09/18/89	117	1025	1500	1500	1500			1625	1525	1800	1825		
09/25/89	118												
10/02/89	119												
10/09/89	120												
10/16/89	121												
10/23/89	122												
10/30/89	123												
11/06/89	124												
11/13/89	125												
11/20/89	126												
11/27/89	127												
12/04/89	128												
12/11/89	129												
12/18/89	130	1150			1600			1450	1250	1600	1700		
12/25/89	131												

TABLE 4
Plasma total thyronine (T4) concentrations (ug/ml)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WKS												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	0.096	0.121	0.093	0.093	0.091	0.092	0.091	0.121	0.097	0.097	0.082	0.097
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17	0.092	0.112	0.098	0.098	0.094	0.087	0.099	0.089	0.086	0.086	0.087	0.068
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21	0.097	0.091	0.082	0.082	0.092	0.085	0.102	0.121	0.084	0.096	0.089	0.096
11/23/87	22	0.072	0.082	0.080	0.075	0.084	0.073	0.094	0.083	0.077	0.089	0.086	0.075
11/30/87	23	0.077	0.089	0.075	0.068	0.078	0.073	0.078	0.088	0.073	0.080	0.089	0.083
12/07/87	24												
12/14/87	25												
12/21/87	26	0.083	0.089	0.091	0.078	0.087	0.074	0.094	0.080	0.078	0.088	0.090	0.077
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	0.087	0.091	0.092	0.079	0.090	0.082	0.064	0.088	0.097	0.086	0.099	0.081
01/25/88	31	0.077	0.080	0.072	0.068	0.071	0.062	0.058	0.065	0.073	0.071	0.063	0.064
02/01/88	32												
02/08/88	33												
02/15/88	34												
02/22/88	35	0.111	0.091	0.085	0.079	0.080	0.095	0.072	0.080	0.063	0.063	0.065	0.070
02/29/88	36	0.075	0.075	0.080	0.073	0.062	0.074	0.049	0.070	0.057	0.068	0.061	0.049
03/07/88	37	0.080	0.088	0.066	0.057	0.071	0.067	0.046	0.075	0.062	0.052	0.057	0.049
03/14/88	38	0.073	0.085	0.088	0.064	0.081	0.086	0.054	0.068	0.066	0.058	0.072	0.043
03/21/88	39	0.069	0.078	0.068	0.061	0.071	0.062	0.061	0.082	0.056	0.060	0.079	0.041
03/28/88	40												
04/04/88	41												
04/11/88	42	0.068	0.069	0.065	0.056	0.060	0.048	0.055	0.051	0.044	0.075	0.066	0.033
04/18/88	43	0.077	0.088	0.094	0.078	0.073	0.079	0.072	0.074	0.054	0.066	0.080	0.040
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	0.059	0.074	0.079	0.044	0.052	0.058	0.047	0.049	0.049	0.039	0.048	0.034
05/23/88	48	0.066	0.075	0.077	0.045	0.064	0.065	0.030	0.059	0.054	0.046	0.054	0.029
05/30/88	49												
06/06/88	50	0.074	0.109	0.091	0.066	0.071	0.081	0.058	0.065	0.060	0.0603	0.056	0.043
06/13/88	51	0.054	0.072	0.050	0.041	0.043	0.046	0.044	0.062	0.041	0.056	0.047	0.033
06/20/88	52	0.044	0.067	0.044	0.041	0.038	0.062	0.041	0.060	0.041	0.040	0.031	0.030
06/27/88	53												
07/04/88	54	0.054	0.069	0.071	0.046	0.046	0.057	0.062	0.080	0.058	0.070	0.059	0.051
07/11/88	55	0.058	0.074	0.056	0.050	0.050	0.059	0.057	0.066	0.055	0.064	0.068	0.045
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.054	0.056	0.065	0.034	0.048	0.048	0.092	0.070	0.039	0.060	0.049	0.042
08/22/88	61	0.088	0.058	0.077	0.048	0.041	0.051	0.111	0.134	0.043	0.056	0.052	0.044
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	0.061	0.054	0.054	0.059	0.045	0.068	0.079	0.079	0.054	0.071	0.065	0.062
09/26/88	66	0.080	0.104	0.104	0.073	0.075	0.092	0.089	0.100	0.060	0.075	0.089	0.074
10/03/88	67	0.074	0.082	0.059	0.055	0.068	0.076	0.065	0.068	0.052	0.067	0.058	0.054
10/10/88	68	0.051	0.067	0.045	0.036	0.045	0.050	0.055	0.035	0.032	0.047	0.036	0.047

TABLE 4
Plasma total thyronine (T4) concentrations (ug/ml)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WKS												
10/17/88	69	0.046	0.062	0.062	0.044	0.037	0.054	0.057	0.062	0.052	0.046	0.061	0.042
10/24/88	70												
10/31/88	71	0.048	0.058	0.048	0.047	0.047	0.064	0.056	0.062	0.039	0.059	0.041	0.048
11/07/88	72	0.052	0.073	0.060	0.054	0.067	0.068	0.081	0.065	0.043	0.073	0.061	0.055
11/14/88	73	0.042	0.054	0.038	0.038	0.030	0.043	0.049	0.052	0.036	0.049	0.038	0.036
11/21/88	74	0.046	0.070	0.065	0.064	0.052	0.066	0.070	0.072	0.055	0.073	0.068	0.055
11/28/88	75	0.043	0.051	0.043	0.050	0.037	0.045	0.057	0.063	0.046	0.054	0.061	0.042
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	0.094	0.100	0.076	0.081	0.078	0.095	0.091	0.103	0.056	0.081	0.082	0.076
01/02/89	80	0.072	0.067	0.086	0.071	0.073	0.086	0.090	0.082	0.082	0.096	0.054	0.077
01/09/89	81												
01/16/89	82												
01/23/89	83	0.043	0.042	0.039	0.044	0.043	0.048	0.038	0.045	0.030	0.069	0.037	0.039
01/30/89	84	0.051	0.068	0.065	0.043	0.046	0.078	0.036	0.049	0.041	0.062	0.038	0.033
02/06/89	85	0.051	0.053	0.046	0.035	0.035	0.048	0.040	0.052	0.036	0.038	0.026	0.040
02/13/89	86												
02/20/89	87	0.057	0.057	0.053	0.060	0.051	0.067	0.044	0.068	0.040	0.057	0.041	0.055
02/27/89	88	0.057	0.062	0.053	0.044	0.045	0.063	0.033	0.048	0.039	0.055	0.032	0.042
03/06/89	89	0.059	0.060	0.057	0.039	0.047	0.068	0.036	0.055	0.044	0.056	0.032	0.037
03/13/89	90	0.037	0.047	0.030	0.020	0.024	0.046	0.020	0.048	0.023	0.034	0.023	0.022
03/20/89	91	0.045	0.044	0.039	0.030	0.040	0.045	0.038	0.023	0.035	0.054	0.025	0.032

TABLE 4
Plasma total thyronine (T4) concentrations (ug/ml)

		GROUP C (artificial light)						GROUP D (natural light)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WKS												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	0.081	0.086	0.106	0.083	0.087	0.109	0.077	0.092	0.039	0.058	0.072	0.044
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17	0.083	0.082	0.080	0.077	0.078	0.110	0.075	0.111	0.054	0.063	0.085	0.057
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21	0.066	0.060	0.078	0.077	0.071	0.094	0.060	0.092	0.037	0.054	0.077	0.050
11/23/87	22	0.048	0.044	0.071	0.057	0.070	0.082	0.055	0.087	0.036	0.062	0.087	0.047
11/30/87	23	0.047	0.045	0.070	0.059	0.067	0.082	0.047	0.079	0.046	0.063	0.073	0.058
12/07/87	24												
12/14/87	25												
12/21/87	26	0.065	0.070	0.084	0.079	0.073	0.083	0.074	0.085	0.064	0.075	0.087	0.068
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	0.062	0.086	0.118	0.067	0.092	0.086	0.091	0.105	0.083	0.079	0.104	0.065
01/25/88	31	0.070	0.055	0.079	0.084	0.064	0.069	0.087	0.088	0.076	0.073	0.088	0.069
02/01/88	32												
02/08/88	33												
02/15/88	34												
02/22/88	35	0.072	0.068	0.103	0.076		0.090	0.090	0.089	0.080	0.079	0.089	0.063
02/29/88	36	0.063	0.071	0.085	0.061		0.076	0.084	0.079	0.070	0.074	0.082	0.057
03/07/88	37	0.072	0.080	0.095	0.074		0.069	0.094	0.075	0.062	0.059	0.070	0.051
03/14/88	38	0.063	0.077	0.087	0.062	0.080	0.087	0.078	0.071	0.065	0.070	0.068	0.058
03/21/88	39	0.080	0.055	0.087	0.058	0.075	0.080	0.083	0.073	0.066	0.083		0.047
03/28/88	40												
04/04/88	41												
04/11/88	42	0.070	0.062	0.070	0.054	0.062	0.076	0.081	0.067	0.063	0.055	0.067	0.050
04/18/88	43	0.086	0.093	0.079	0.081		0.088	0.105	0.132	0.102	0.101	0.133	0.097
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	0.064	0.055	0.076	0.060		0.077	0.083	0.067	0.062	0.064	0.062	0.068
05/23/88	48	0.068	0.053	0.079	0.067		0.076	0.077	0.058	0.054	0.074	0.074	0.056
05/30/88	49												
06/06/88	50	0.089	0.086	0.100	0.079		0.099	0.079	0.061	0.070	0.077	0.080	0.054
06/13/88	51	0.055	0.047	0.067	0.045		0.064	0.072	0.059	0.061	0.064	0.073	0.048
06/20/88	52	0.070	0.062	0.061	0.046		0.054	0.065	0.057	0.063	0.064	0.063	0.041
06/27/88	53												
07/04/88	54	0.068	0.048	0.070	0.056			0.066	0.059	0.053	0.060	0.078	0.051
07/11/88	55	0.042	0.057	0.070	0.073			0.098	0.075	0.089	0.090	0.097	0.058
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.045	0.042	0.045	0.046			0.059	0.055	0.044	0.053	0.062	0.047
08/22/88	61	0.086	0.039	0.046	0.037			0.067	0.052	0.057	0.062	0.063	0.046
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	0.034	0.045	0.056	0.049			0.046	0.048	0.039	0.048	0.072	0.030
09/26/88	66	0.058	0.075	0.065	0.061			0.036	0.073	0.033	0.078	0.092	0.044
10/03/88	67	0.057	0.056	0.063	0.059			0.060	0.061	0.045	0.079	0.085	0.031
10/10/88	68	0.032	0.032	0.046	0.042			0.055	0.058	0.030	0.052	0.056	0.024

TABLE 4
Plasma total thyronine (T4) concentrations (ug/ml)

		GROUP C (artificial light)						GROUP D (natural light)					
	sheep	16	54	56	107	98	118	30	31	176	202	84	243
DATE	WKS												
10/17/88	69	0.030	0.026	0.042	0.034			0.058	0.051	0.037	0.060	0.072	0.048
10/24/88	70												
10/31/88	71	0.028	0.023	0.052	0.044			0.046	0.051	0.036	0.067	0.064	0.039
11/07/88	72	0.032	0.036	0.050	0.044			0.051	0.052	0.054	0.070	0.071	0.041
11/14/88	73	0.023	0.042	0.020	0.029			0.057	0.073	0.043	0.061	0.091	0.027
11/21/88	74	0.043	0.031	0.072	0.053			0.072	0.052	0.045	0.070	0.075	0.038
11/28/88	75	0.038	0.040	0.047	0.029			0.059	0.066	0.040	0.055	0.067	0.037
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	0.095	0.071	0.089	0.087			0.082	0.090	0.079	0.115	0.082	
01/02/89	80	0.074	0.082	0.095	0.097			0.078	0.072	0.052	0.092	0.091	
01/09/89	81												
01/16/89	82												
01/23/89	83	0.040	0.037	0.067	0.044			0.079	0.048	0.054	0.060	0.072	
01/30/89	84	0.062	0.039	0.062	0.059			0.075	0.043	0.054	0.061	0.074	
02/06/89	85	0.048	0.040	0.053	0.048			0.081	0.037	0.048	0.053	0.059	
02/13/89	86												
02/20/89	87	0.062	0.053	0.073	0.067			0.097	0.053	0.065	0.064	0.090	
02/27/89	88	0.066	0.055	0.087	0.062			0.095	0.063	0.059	0.074	0.069	
03/06/89	89	0.085	0.043	0.072	0.068			0.081	0.079	0.057	0.069	0.060	
03/13/89	90	0.040	0.025	0.042	0.038			0.072	0.066	0.062	0.060	0.060	
03/20/89	91	0.050	0.028	0.062	0.044			0.058	0.048	0.048	0.053	0.044	

TABLE 5
Plasma total triiodothyronine (T3) concentrations (ng/ml)

		----------GROUP A (12L:12D)--------						-----GROUP B (artificial light)----					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	1.45	1.49	1.83	1.89	1.80	1.49	1.41	1.73	1.84	1.81	1.35	1.64
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17	1.44	1.89	1.91	2.02	1.81	1.85	2.85	1.79	1.78	1.78	1.89	2.10
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21	1.44	1.55	1.56	1.76	1.80	1.34	1.70	1.70	1.81	1.65	1.88	1.78
11/23/87	22	1.33	1.41	1.47	1.20	1.39	1.08	1.65	1.31	1.29	1.18	1.36	1.34
11/30/87	23	1.48	1.24	1.59	1.29	1.26	1.13	1.57	1.57	1.85	1.23	2.04	1.38
12/07/87	24												
12/14/87	25												
12/21/87	26	1.72	1.65	2.39	1.86	1.75	1.83	1.89	1.58	1.54	1.89	1.60	1.32
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	1.49	1.35	1.38	1.15	1.63	1.04	0.92	1.14	1.60	1.04	1.09	0.90
01/25/88	31	1.47	1.50	1.41	1.43	1.10	1.06	1.49	1.31	1.30	1.36	0.75	0.68
02/01/88	32												
02/08/88	33												
02/15/88	34												
02/22/88	35	1.44	1.47	1.22	0.93	1.37	1.55	1.09	0.90	0.92	0.89	0.91	0.83
02/29/88	36	1.23	1.24	1.34	0.95	[illegible]	1.17	0.69	0.94	0.81	0.94	0.70	0.57
03/07/88	37	1.14	0.92	0.91	0.98	[illegible]	0.95	0.55	0.84	0.75	0.74	0.67	0.66
03/14/88	38	0.96	1.10	1.47	1.03	1.33	1.02	0.74	0.89	0.92	0.88	0.89	0.59
03/21/88	39	1.04	1.12	0.84	0.89	1.14	0.94	0.65	0.94	1.03	0.76	0.68	0.53
03/28/88	40												
04/04/88	41												
04/11/88	42	1.36	1.15	1.32	1.02	0.80	0.95	1.00	0.87	1.02	1.22	0.82	0.54
04/18/88	43	1.32	1.30	1.39	0.96	1.06	1.36	1.10	1.27	1.18	1.08	1.07	0.60
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	0.92	0.89	0.89	0.94	0.79	1.19	0.73	0.71	0.62	0.63	0.60	0.42
05/23/88	48	0.58	0.73	0.87	0.71	0.98	0.89	0.66	0.60	0.65	0.74	[illegible]	0.47
05/30/88	49												
06/06/88	50	1.20	1.10	1.27	1.05	1.16	1.27	0.84	0.71	0.76	0.91	0.67	0.70
06/13/88	51	0.98	0.77	0.99	0.86	0.91	1.21	0.85	0.87	0.60	0.69	0.50	0.53
06/20/88	52	0.92	0.88	1.00	0.94	0.73	1.07	0.63	0.75	0.69	0.69	0.51	0.36
06/27/88	53												
07/04/88	54	1.02	0.79	1.26	0.66	0.81	0.77	0.80	0.90	0.69	0.88	0.54	0.63
07/11/88	55	0.75	0.72	1.03	0.69	0.77	0.90	1.12	0.92	0.93	0.86	0.69	0.60
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	1.25	0.58	0.62	0.46	0.69	0.66	0.95	0.81	0.51	0.74	0.58	0.58
08/22/88	61	1.06	0.59	0.75	0.62	0.77	0.68	0.72	0.75	0.63	0.73	0.61	0.72
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	0.98	0.75	0.65	0.87	0.74	0.82	0.89	0.95	0.80	0.99	0.69	0.64
09/26/88	66	1.43	1.02	1.39	1.15	1.19	1.39	1.93	1.55	0.87	1.37	1.46	1.23
10/03/88	67	1.24	1.10	1.24	1.09	1.11	1.31	1.59	1.57	1.15	1.48	1.03	
10/10/88	68	0.85	0.59	0.80	0.63	0.59	1.00	1.02	0.84	0.77	0.40	0.31	0.77

TABLE 5
Plasma total triiodothyronine (T3) concentrations (ng/ml)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
10/17/88	69	0.97	0.69	0.60	0.45	0.64	0.72	0.98	0.85	0.80	0.59	0.91	0.75
10/24/88	70												
10/31/88	71	0.71	0.59	0.50	0.54	0.60	0.60	0.96	0.74	0.69	0.55	0.50	0.69
11/07/88	72	0.86	1.19	1.21	1.23	0.98	1.21	1.35	1.29	1.33	1.37	1.13	1.22
11/14/88	73	0.60	0.47	0.66	0.68	0.40	0.38	1.02	0.78	0.56	0.60	0.69	0.53
11/21/88	74	1.16	1.12	1.07	1.36	1.22	1.31	1.13	1.04	1.08	1.91	1.42	0.63
11/28/88	75	1.00	0.73	0.62	0.94	0.76	0.84	1.02	0.96	0.90	1.09	1.23	0.85
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	1.53	1.48	1.16	1.31	1.13	1.51	1.51	1.58	1.17	1.43	1.47	1.16
01/02/89	80	1.24	0.99	1.16	1.11	0.89	1.23	1.40	1.50	1.04	1.39	0.73	1.10
01/09/89	81												
01/16/89	82												
01/23/89	83	0.96	0.82	0.70	1.09	0.57	0.75	1.04	0.73	0.80	1.88	0.73	0.66
01/30/89	84	0.94	0.88	0.81	0.74	0.72	1.27	0.72	0.74	0.85	1.14	0.52	0.85
02/05/89	85	0.83	0.93	0.75	0.85	0.83	1.02	0.96	0.78	0.75	0.76	0.66	0.79
02/13/89	86												
02/20/89	87	1.13	1.04	0.83	0.77	0.84	0.79	0.81	0.66	0.53	0.93	0.67	0.66
02/27/89	88	0.76	0.92	0.79	0.69	0.67	0.86	0.59	0.79	0.68	0.93	0.53	0.56
03/06/89	89	0.92	0.78	0.69	0.61	0.67	0.73	0.72	0.67	0.65	0.67	0.63	0.59
03/13/89	90	0.63	0.73	0.33	0.44	0.57	0.67	0.27	0.46	0.39	0.66	0.31	0.41
03/20/89	91	0.95	0.68	0.80	1.02	0.71	0.72	0.64	0.56	0.64	0.86	0.35	0.58

TABLE 5
Plasma total triiodothyronine (T3) concentrations (ng/ml)

		GROUP C (artificial light)						GROUP D (Natural light)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	1.52	1.57	1.82	1.47	1.50	1.65	1.02	1.21	0.87	1.12	0.86	0.66
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17	1.66	1.77	2.08	1.58	1.78	2.22	1.34	1.77	0.93	1.02	1.47	1.13
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21	1.52	1.28	1.31	1.31	1.39	1.91	1.16	1.65	1.02	1.05	1.11	1.28
11/23/87	22	0.72	0.80	1.02	0.91	0.87	1.15	0.87	1.29	0.83	0.73	1.37	0.65
11/30/87	23	0.96	1.24	1.50	1.33	1.18	2.08	1.44	1.01	1.05	1.26	1.04	0.91
12/07/87	24												
12/14/87	25												
12/21/87	26	1.10	1.61	1.73	1.30	1.34	1.52	1.45	1.86	1.13	1.30	1.48	1.21
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	1.54	1.41	1.82	1.66	1.21	1.80	1.26	1.67	1.07	1.30	1.53	1.37
01/25/88	31	1.48	1.29	1.89	1.39	1.14	1.49	2.09	1.71	1.10	1.19	1.47	1.34
02/01/88	32												
02/08/88	33												
02/15/88	34												
02/22/88	35	1.49	1.51	1.87	1.36		1.49	1.13	1.09	1.27	1.34	1.04	1.20
02/29/88	36	1.16	0.76	1.50	1.22		1.35	1.46	1.55	1.27	1.37	1.21	1.07
03/07/88	37	1.17	0.86	1.44	0.99		1.16	1.47	1.31	1.15	1.51	0.90	0.91
03/14/88	38	1.24	1.65	1.49	1.05	1.84	1.12	1.69	1.14	1.19	0.82	1.09	1.05
03/21/88	39	1.38	0.94	1.43	1.22	1.02	1.47	1.86	1.35	1.57	1.42	1.16	0.92
03/28/88	40												
04/04/88	41												
04/11/88	42	1.54	1.35	1.55	1.03		1.30	1.49	0.89	0.85	0.95	1.06	0.95
04/18/88	43	1.67	1.41	1.02	1.10		1.61	1.68	1.64	1.70	1.61	1.25	1.28
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	1.13	0.87	1.11	1.05		1.24	1.49	1.03	0.89	1.02	0.81	0.93
05/23/88	48	1.34	1.08	1.09	1.01		1.55	1.16	1.01	0.94	1.03	0.95	0.98
05/30/88	49												
06/06/88	50	1.37	1.76	1.90	1.36		1.47	1.31	1.01	1.12	1.37	1.11	0.97
06/13/88	51	0.85	1.06	1.32	1.03		0.77	0.95	0.69	0.97	0.99	1.10	0.86
06/20/88	52	1.06	0.64	0.80	0.88		0.93	0.99	0.86	1.07	1.28	1.06	0.78
06/27/88	53												
07/04/88	54	0.90	0.66	0.98	0.83			0.83	0.84	0.86	0.95	0.88	0.79
07/11/88	55	0.95	0.97	1.19	1.14			1.48	1.35	1.37	1.59	1.34	0.76
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.64	0.61	0.42	0.52			0.88	0.94	0.69	0.83	1.00	0.88
08/22/88	61	0.65	0.54	0.69	0.67			1.01	0.77	0.72	1.02	0.85	0.66
08/29/88	62												
09/05/38	63												
09/12/88	64												
09/19/88	65	0.49	0.72	0.81	0.69			0.80	0.75	0.55	0.74	1.04	0.47
09/26/68	66	0.92	1.20	1.06	1.22			1.00	1.18	0.82	1.37	1.31	0.77
10/03/88	67	0.91	0.96		0.93			1.16	1.22	0.79	1.16	1.15	0.68
10/10/88	68	0.47	0.58	0.60	0.73			0.91	0.79	0.61	1.01	0.95	0.54

TABLE 5
Plasma total triiodothyronine (T3) concentrations (ng/ml)

		GROUP C (artificial light)						GROUP D (Natural light)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
10/17/88	69	0.54	0.41	0.79	0.33			0.90	0.59	0.42	0.85	0.87	0.87
10/24/88	70												
10/31/88	71	0.47	0.24	0.63	0.56			0.66	0.73	0.56	0.75	0.56	0.46
11/07/88	72	0.60	0.94	1.07	0.88			1.03	1.18	0.79	1.15	1.07	0.93
11/14/88	73	0.49	0.59	0.41	0.48			1.12	1.43	0.95	1.48	1.07	0.76
11/21/88	74	0.76	0.78	0.85	0.95			1.16	1.06	1.12	1.05	0.84	0.77
11/28/88	75	0.60	0.65	0.79	0.70			0.87	1.18	1.14	1.21	1.10	0.87
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	2.44	1.41	1.57	1.48			1.68	1.85	1.76	2.03	1.32	
01/02/89	80	1.02	1.47	1.35	1.42			1.14	1.26	0.95	1.38	1.04	
01/09/89	81												
01/16/89	82												
01/23/89	83	0.89	1.15	1.61	0.70			1.55	1.23	1.05	1.20	1.30	
01/30/89	84	1.12	0.90	1.32	0.96			1.32	1.13	1.05	1.28	1.25	
02/06/89	85	1.03	0.76	0.85	1.35			1.70	1.23	1.57	1.80	0.94	
02/13/89	86												
02/20/89	87	1.07	0.84	0.93	1.09			1.41	1.00	1.22	1.16	1.20	
02/27/89	88	1.01	0.88	1.41	1.00			1.52	1.22	1.24	1.37	1.15	
03/06/89	89	1.28	0.73	1.01	1.24			1.31	1.22	1.26	1.39	0.81	
03/13/89	90	0.63	0.58	0.64	0.83			1.43	1.15	1.29	1.18	1.14	
03/20/89	91	0.96	0.67	0.86	0.79			1.13	1.05	0.79	1.01	0.87	

TABLE 6
Plasma free T4 concentrations (ng/dl)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	1.068	0.914	0.951	0.995	0.974	1.030	1.037	1.257	0.948	0.992	0.971	1.175
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17												
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21												
11/23/87	22	0.999	0.938	0.964	0.956	0.965	1.009	1.018	1.178	1.123	1.033	1.391	0.801
11/30/87	23	0.837	1.085	0.745	0.542	0.889	0.930	0.850	1.373	0.988	0.758	1.065	0.843
12/07/87	24												
12/14/87	25												
12/21/87	26												
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	0.916	0.991	1.034	0.761	0.805	0.939	0.501	0.878	1.106	0.770	1.223	0.774
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34	0.715	1.032	0.935	0.901	1.042	1.215	0.674	1.074	0.908	0.914	0.796	0.590
02/22/88	35	1.380	0.979	1.130	1.050	0.938	0.973	0.818	1.105	0.683	0.586	0.722	0.738
02/29/88	36												
03/07/88	37												
03/14/88	38	0.977	1.081	1.415	0.910	0.954	1.222	0.752	1.111	0.722	0.727	1.004	0.442
03/21/88	39	0.949	1.003	0.901	0.760	0.810	0.792	0.697	1.072	0.655	0.707	0.993	0.432
03/28/88	40												
04/04/88	41												
04/11/88	42	0.812	0.564	0.874	0.757	0.882	0.616	0.878	0.629	0.613	0.998	0.796	0.531
04/18/88	43	1.257	1.296	1.461	1.268	1.277	1.297	1.169	1.214	0.832	0.920	1.281	0.532
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	0.795	0.824	1.122	0.613	1.056	0.768	0.684	0.909	0.729	0.562	0.687	0.435
05/23/88	48	0.921	0.914	0.991	0.727	1.046	0.758	0.611	0.932	0.782	0.559	0.816	0.280
05/30/88	49												
06/06/88	50												
06/13/88	51	0.690	0.931	0.613	0.570	0.707	0.690	0.570	0.867	0.488	0.779	0.844	0.464
06/20/88	52	0.559	0.730	0.721	0.690	0.545	0.974	0.398	0.869	0.568	0.796	0.625	0.396
06/27/88	53												
07/04/88	54	0.656	0.578	0.812	0.676	0.586	0.604	0.621	0.918	0.559	0.938	1.016	0.631
07/11/88	55	0.556	0.811	0.513	0.605	0.559	0.713	0.668	0.959	0.710	0.635	0.981	0.566
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.678	0.692	0.941	0.434	0.735	[illegible]	1.028	1.031	0.458	0.759	0.937	0.661
08/22/88	61	0.709	0.621	0.817	0.602	0.639	[illegible]	0.745	1.147	0.452	0.623	0.898	0.586
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	1.250	0.956	1.048	1.301	0.942	1.045	1.439	1.603	1.091	1.267	1.431	1.154
09/26/88	66	1.603	2.012	2.380	1.849	1.527	2.167	1.882	2.468	1.260	1.528	2.236	1.752
10/03/88	67												
10/10/88	68	1.155	1.306	1.086	0.888	0.995	1.160	1.332	0.937	0.773	1.014	1.056	1.099

TABLE 6
Plasma free T4 concentrations (ng/dl)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
10/17/88	69	1.005	1.394	1.479	1.058	0.892	0.986	1.359	1.694	1.186	1.276	1.549	1.036
10/24/88	70												
10/31/88	71	0.903	0.941	0.956	0.900	0.893	0.973	1.025	1.274	0.759	1.027	1.141	0.848
11/07/88	72	0.897	1.222	1.094	1.161	1.061	1.097	1.294	1.449	0.803	1.225	1.312	1.029
11/14/88	73	0.823	1.079	0.819	1.012	0.785	0.933	1.213	1.208	0.849	0.952	1.124	0.918
11/21/88	74												
11/28/88	75												
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	1.015	1.283	0.999	1.319	0.985	1.147	1.117	1.297	0.643	1.004	1.661	0.839
01/02/89	80	0.982	0.990	1.053	0.823	0.800	0.833	0.815	1.000	0.657	0.879	1.043	0.801
01/09/89	81												
01/16/89	82												
01/23/89	83	0.613	0.470	0.555	0.567	0.488	0.468	0.408	0.618	0.342	0.786	0.590	0.418
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87	0.690	0.819	0.745	0.932	0.840	1.061	0.676	1.062	0.507	0.721	0.525	0.630
02/27/89	88	0.699	0.791	0.629	0.661	0.624	0.767	0.383	0.681	0.460	0.632	0.567	0.437
03/06/89	89	0.635	0.780	0.689	0.543	0.617	0.866	0.511	0.710	0.536	0.528	0.466	0.449
03/13/89	90	0.631	0.824	0.670	0.601	0.522	1.093	0.400	0.686	0.497	0.617	0.633	0.447
03/20/89	91	0.596	0.667	0.778	0.653	0.621	0.643	0.532	0.432	0.542	0.683	0.471	0.477
03/27/89	92												

TABLE 6
Plasma free T4 concentrations (ng/dl)

		GROUP C (artificial light)						GROUP D (NATURAL)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	0.967	0.866	1.210	0.848		1.195	0.629	0.978	0.329	0.509	0.610	0.486
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17												
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21												
11/23/87	22	0.484	0.711	0.717	0.683		0.774	0.514	0.876	0.326	0.675	[illegible]02	0.675
11/30/87	23	0.552	0.494	0.581	0.456		0.890	0.522	1.034	0.501	0.701	0.783	0.659
12/07/87	24												
12/14/87	25												
12/21/87	26												
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	0.685	1.023	1.445	0.665		0.929	0.824	1.179	0.827	0.881	1.042	0.737
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34	0.850	0.953	1.072	1.029		0.937	1.152	1.084	0.913	0.854	1.118	0.901
02/22/88	35	0.996	0.972	1.123	0.917		1.113	0.900	1.098	1.107	1.026	1.114	0.723
02/29/88	36												
03/07/88	37												
03/14/88	38	0.944	1.071	1.208	0.779		1.075	0.963	1.110	1.015	1.080	0.947	0.741
03/21/88	39	0.963	0.752	1.252	0.484		0.858	0.978	0.890	0.920	1.070	1.066	0.623
03/28/88	40												
04/04/88	41												
04/11/88	42	0.999	0.837	0.855	0.693		1.095	0.835	0.801	0.838	0.637	0.909	0.570
04/18/88	43	1.353	1.441	1.541	1.267		1.528	1.385	2.198	1.737	1.476	2.058	1.480
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	1.127	1.007	0.974	0.942		1.276	1.092	1.012	0.858	0.827	0.914	0.741
05/23/88	48	1.045	1.029	1.188	0.853		1.184	0.807	0.894	0.710	0.750	0.963	0.535
05/30/88	49												
06/06/88	50												
06/13/88	51	0.737	0.707	0.903	0.502		0.798	0.613	0.860	0.654	0.682	0.742	0.431
06/20/88	52	0.908	0.706	0.694	0.613		0.897	0.661	0.787	0.580	0.645	0.645	0.476
06/27/88	53												
07/04/88	54	0.658	0.601	0.799	0.591			0.571	0.690	0.494	0.637	0.896	0.673
07/11/88	55	0.577	0.846	0.769	0.703			1.023	1.262	1.152	1.074	1.143	0.724
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.671	0.680	0.651	0.627			0.573	0.742	0.417	0.550	0.630	0.665
08/22/88	61	0.721	0.553	0.515	0.360			0.601	0.524	0.427	0.529	0.590	0.401
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	0.775	1.056	0.915	0.727			0.725	0.954	0.537	0.838	1.052	0.566
09/26/88	66	1.247	1.590	1.211	0.914			0.950	1.628	0.751	1.702	1.853	0.816
10/03/88	67												
10/10/88	68	0.807	0.843	1.025	0.945			1.112	1.067	0.589	1.003	1.204	0.512

TABLE 6
Plasma free T4 concentrations (ng/dl)

		GROUP C (artificial light)						GROUP D (NATURAL)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
10/17/88	69	0.724	0.686	1.013	0.572			0.971	1.157	0.638	1.021	1.209	0.831
10/24/88	70												
10/31/88	71	0.524	0.585	1.009	0.800			0.608	0.927	0.611	1.001	1.177	0.699
11/07/88	72	0.556	0.709	0.882	0.664			0.680	0.973	0.804	0.939	1.121	0.654
11/14/88	73	0.593	0.852	0.641	0.662			0.758	1.052	0.705	0.866	1.233	0.499
11/21/88	74												
11/28/88	75												
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	1.263	0.993	1.223	0.989			1.026	1.308	1.051	1.812	0.823	
01/02/89	80	0.876	1.263	1.130	1.027			0.837	1.071	0.535	0.913	1.034	
01/09/89	81												
01/16/89	82												
01/23/89	83	0.458	0.622	0.774	0.374			0.791	0.953	0.635	0.632	0.908	
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87	1.078	0.964	0.960	0.938			1.328	1.008	0.895	0.923	1.421	
02/27/89	88	0.796	0.795	1.210	0.715			1.037	0.912	0.636	1.062	1.150	
03/06/89	89	1.346	0.758	0.964	1.038			1.055	1.184	0.795	0.928	0.893	
03/13/89	90	0.915	0.723	0.882	0.716			0.936	1.027	0.639	0.869	1.029	
03/20/89	91	0.788	0.506	0.949	0.735			0.795	0.792	0.704	0.712	0.767	
03/27/89	92												

TABLE 7
Plasma free T3 concentrations (pg/ml)

		GROUP A (12L:12D)						GROUP B (artificial light					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	1.716	1.142	1.868	2.498	1.759	1.124	1.463	1.866	2.165	1.652	1.303	2.521
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17												
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21												
11/23/87	22	1.332	1.636	0.995	1.058	0.800	0.722	1.811	1.232	1.493	1.390	1.506	1.492
11/30/87	23	1.069	1.287	1.476	1.290	1.360	1.068	0.903	1.881	1.519	1.366	2.738	2.106
12/07/87	24												
12/14/87	25												
12/21/87	26												
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	2.137	1.730	1.488	1.069	1.521	0.853	0.945	1.369	2.266	0.838	1.041	0.982
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34	0.988	0.900	1.439	1.121	1.480	1.682	1.033	1.456	0.917	1.136	[illegible]	[illegible]
02/22/88	35	1.602	1.467	1.682	0.859	1.652	2.273	0.835	0.645	0.500	0.500	0.500	0.561
02/29/88	36												
03/07/88	37												
03/14/88	38	1.758	1.367	2.238	1.389	2.228	2.438	0.697	1.229	1.595	0.676	1.133	0.692
03/21/88	39	1.784	1.902	1.158	1.275	1.394	0.707	0.500	1.242	2.106	1.263	0.735	0.500
03/28/88	40												
04/04/88	41												
04/11/88	42	1.610	1.086	1.421	1.397	0.824	0.571	1.331	0.856	1.338	1.464	0.541	0.500
04/18/88	43	2.045	2.100	1.858	1.302	1.439	2.377	2.014	1.732	1.868	1.016	1.741	0.500
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	0.842	1.482	1.253	2.148	1.542	2.543	0.981	0.500	0.500	0.715	0.771	0.601
05/23/88	48	[illegible]	[illegible]	1.207	0.500	1.313	1.736	0.985	0.624	1.080	0.629	0.500	1.047
05/30/88	49												
06/06/88	50												
06/13/88	51	1.191	1.277	1.208	0.692	1.344	1.624	0.657	1.101	0.995	1.506	0.500	0.500
06/20/88	52	0.988	1.143	1.467	1.940	0.803	1.640	0.598	0.500	0.655	1.709	0.889	0.765
06/27/88	53												
07/04/88	54	1.226	0.693	1.548	0.829	0.989	0.671	0.574	1.193	0.893	1.163	0.500	0.998
07/11/88	55	1.020	0.812	0.730	0.500	0.500	0.877	0.864	0.560	1.174	0.500	0.500	0.593
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.704	0.500	1.254	0.500	1.186	1.042	1.091	0.951	0.500	1.205	0.500	1.155
08/22/88	61												
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	1.124	1.114	1.929	2.139	2.468	3.256	2.698	2.356	2.678	1.644	1.784	2.050
09/26/88	66	4.306	3.620	4.772	5.494	3.552	3.904	6.350	4.763	2.209	4.396	3.858	3.851
10/03/88	67												
10/10/88	68	3.065	2.479	2.916	2.603	1.803	2.732	3.203	2.532	2.584	1.393	1.671	3.902

TABLE 7
Plasma free T3 concentrations (pg/ml)

		GROUP A (12L:12D)						GROUP B (artificial light					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WK												
10/17/88	69	3.198	3.199	2.388	2.235	1.450	2.250	4.036	2.452	3.947	1.114	3.858	1.374
10/24/88	70												
10/31/88	71	2.150	2.933	1.356	2.828	2.380	3.140	3.230	2.239	1.706	2.135	2.139	3.558
11/07/88	72	1.321	2.186	2.294	2.987	2.495	3.238	4.928	3.781	2.695	2.923	2.626	2.583
11/14/88	73	0.808	0.898	0.815	2.055	0.792	0.513	1.565	1.760	2.642	1.546	2.085	1.996
11/21/88	74												
11/28/88	75												
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	1.657	1.062	0.954	1.732	1.159	2.240	1.227	1.509	1.031	6.864	2.228	1.573
01/02/89	80	1.397	1.083	0.917	1.497	0.944	1.372	1.584	1.535	1.480	3.725	1.057	1.083
01/09/89	81												
01/16/89	82												
01/23/89	83												
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87	2.343	0.759	0.500	0.500	0.923	0.644	0.300	0.500	0.667	0.500	0.500	0.580
02/27/89	88	0.500	0.695	0.500	0.500	2.972	1.862	1.272	0.604	0.660	1.701	1.323	1.185
03/06/89	89	1.208	1.258	0.500	1.717	0.500	0.500	0.500	0.500	0.500	1.925	0.642	0.500
03/13/89	90	0.700	2.656	0.500	0.500	0.858	0.500	0.500	0.500	0.500	0.520	0.500	0.500
03/20/89	91	0.776	1.542	0.500	2.302	0.879	1.333	0.500	0.500	1.344	0.500	0.500	1.047
03/27/89	92												

TABLE 7
Plasma free T3 concentrations (pg/ml)

		GROUP C (artificial light)						GROUP D (Natural light)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	1.265	1.796	1.804	1.235		1.597	0.859	1.085	0.500	0.500	0.500	0.500
09/28/87	14												
10/05/87	15												
10/12/87	16												
10/19/87	17												
10/26/87	18												
11/02/87	19												
11/09/87	20												
11/16/87	21												
11/23/87	22	0.500	0.500	0.500	0.500		1.377	0.500	0.863	0.500	0.500	0.639	0.500
11/30/87	23	0.500	0.656	1.510	0.500		2.667	0.682	0.676	0.500	0.909	1.263	0.583
12/07/87	24												
12/14/87	25												
12/21/87	26												
12/28/87	27												
01/04/88	28												
01/11/88	29												
01/18/88	30	2.194	1.80[illegible]				2.563	1.107	2.439	0.811	1.341	2.277	0.989
01/25/88	31												
02/01/88	32												
02/08/88	33												
02/15/88	34	1.420	2.052	3.14[illegible]	[illegible]52		1.591	[illegible]62	0.958	1.501	1.353	1.577	1.566
02/22/88	35	1.667	2.024	3.719	[illegible].257		1.535	[illegible]	[illegible].703	1.363	1.465	1.192	1.176
02/29/88	36												
03/07/88	37												
03/14/88	38	1.825	2.494	2.021	1.046		2.255	2.962	2.426	1.897	1.553	1.139	1.735
03/21/88	39	2.151	1.645	2.106	1.126		1.664	3.921	1.456	2.344	1.351	2.406	1.091
03/28/88	40												
04/04/88	41												
04/11/88	42	1.888	1.509	1.870	1.527		2.079	2.110	1.311	0.960	1.461	1.661	1.419
04/18/88	43	3.568	2.502	1.599	1.595		2.797	2.950	2.830	2.712	2.480	1.707	1.832
04/25/88	44												
05/02/88	45												
05/09/88	46												
05/16/88	47	2.245	2.127	2.137	2.346		2.754	2.314	2.019	1.707	1.642	1.361	1.793
05/23/88	48	3.272	1.496	2.042	1.663		2.751	1.928	1.511	0.885	1.430	1.095	1.030
05/30/88	49												
06/06/88	50												
06/13/88	51	1.011	1.538	2.501	0.981		0.869	0.873	0.726	0.881	1.344	1.290	0.575
06/20/88	52	1.083	1.448	1.302	0.786		1.059	1.771	1.863	0.877	1.645	1.695	0.691
06/27/88	53												
07/04/88	54	1.080	0.500	1.036	0.798			0.898	1.173	0.705	0.989	1.060	0.833
07/11/88	55	0.782	0.873	1.086	0.852			2.095	1.929	1.402	1.860	1.482	1.051
07/18/88	56												
07/25/88	57												
08/01/88	58												
08/08/88	59												
08/15/88	60	0.500	0.500	0.500	0.847			0.784	0.857	0.5[illegible]	[illegible]	0.862	0.875
08/22/88	61												
08/29/88	62												
09/05/88	63												
09/12/88	64												
09/19/88	65	0.500	0.958	0.500	0.544			0.721	2.270	1.591	1.897	2.448	0.500
09/26/88	66	3.134	3.476	3.338	3.382			2.878	2.885	0.986	3.718	4.382	2.180
10/03/88	67												
10/10/88	68	0.500	1.599	2.217	2.275			1.566	1.596	0.500	1.975	3.409	0.976

TABLE 7
Plasma free T3 concentrations (pg/ml)

		GROUP C (artificial light)						GROUP D (Natural light)					
	sheep	16	54	56	107	98	118	30	31	176	202	64	243
DATE	WK												
10/17/88	69	2.140	0.500	2.304	1.168			1.078	2.333	0.500	2.101	2.397	1.833
10/24/88	70												
10/31/88	71	1.377	0.500	0.769	1.555			1.174	2.526	1.990	2.600	2.544	1.418
11/07/88	72	1.436	1.360	1.254	0.571			2.329	3.028	1.075	2.551	3.050	0.682
11/14/88	73	0.500	0.589	0.644	0.583			1.094	2.328	0.719	1.244	1.529	0.500
11/21/88	74												
11/28/88	75												
12/05/88	76												
12/12/88	77												
12/19/88	78												
12/26/88	79	3.104	1.317	1.817	1.176			1.408	1.893	1.407	2.932	1.541	
01/02/89	80	1.040	2.231	1.604	1.760			0.926	1.183	0.984	1.331	1.061	
01/09/89	81												
01/16/89	82												
01/23/89	83												
01/30/89	84												
02/06/89	85												
02/13/89	86												
02/20/89	87	2.561	1.233	1.430	1.872			2.392	1.533	2.712	1.408	2.466	
02/27/89	88	1.645	2.092	2.968	1.272			4.175	2.829	2.696	4.233	2.623	
03/06/89	89	2.723	0.915	1.508	2.215			2.895	1.728	1.643	1.961	1.465	
03/13/89	90	2.018	2.449	1.955	2.452			2.862	2.071	1.858	2.428	1.931	
03/20/89	91	0.698	0.667	0.738	2.792			2.285	1.796	1.325	1.782	1.414	
03/27/89	92												

TABLE 8
Plasma progesterone concentrations (ng/ml)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	169	239	20	39	47	81	93	246
DATE	WEEK												
06/29/87	1												
07/06/87	2												
07/13/87	3												
07/20/87	4												
07/27/87	5												
08/03/87	6												
08/10/87	7												
08/17/87	8												
08/24/87	9												
08/31/87	10												
09/07/87	11												
09/14/87	12												
09/21/87	13	0.80					0.17	1.30					
09/28/87	14	0.70					3.48	1.18					
10/05/87	15	1.02					6.24	1.10					
10/12/87	16	0.80					1.39	1.03	1.27	0.04	0.10	0.13	
10/19/87	17	0.76					2.34	1.23					
10/26/87	18	0.58					0.42	1.16					
11/02/87	19	0.30	0.09	7.69	0.14	0.03	2.72	1.27					
11/09/87	20	0.76					2.35	1.29					
11/16/87	21	0.58						1.02	0.16	0.02	0.05	0.15	
11/23/87	22	0.63						1.27					
11/30/87	23	0.28						1.13					
12/07/87	24	0.52	0.12	0.22	0.06	0.02	0.02	0.65					
12/14/87	25	0.62						0.88	4.83	0.02	0.04	0.12	
12/21/87	26	1.04						1.16					
12/28/87	27	1.25	0.09	0.09	0.08	0.03	0.06	1.09					
01/04/88	28	1.08	0.08	0.12	0.02	0.03	0.06	1.19					
01/11/88	29	0.82						1.28	0.26	0.04	0.02	0.04	
01/18/88	30	1.32						0.96					
01/25/88	31	1.03	0.08	0.05	0.04	0.03	0.10	0.82					
02/01/88	32	0.84						1.37	0.20	0.15	0.24		
02/08/88	33	0.80	0.11	0.09	0.03	0.03	0.07	1.22	0.22	0.31	0.19		
02/15/88	34	0.90						1.15	0.28	0.27	0.26	0.22	
02/22/88	35	1.12						1.39	0.18	0.14	0.19	0.22	
02/29/88	36	0.75						1.29	2.99	0.40	0.39	0.35	0.32
03/07/88	37	0.95	0.26	0.38	0.34	0.31	0.37	2.43	0.39	5.59	0.37	0.33	0.29
03/14/88	38	1.41	0.45	0.29	0.37	0.19	0.34	3.40	1.78	6.68	3.61	0.77	0.32
03/21/88	39	3.90	0.37	0.37	0.33	0.23	0.37	7.02	3.71	1.98	5.73	5.89	0.29
03/28/88	40	7.92	0.42	0.30	0.31	0.27	0.32	3.21	0.11	7.87	0.51	0.46	0.31
04/04/88	41	1.23	0.31	0.27	0.36	0.31	0.33	7.11	4.41	0.46	5.24	5.08	0.37
04/11/88	42	1.02	0.29	0.25	0.50	0.27	0.39	1.93	0.37	5.81	0.29	3.72	0.28
04/18/88	43	2.46	0.35	0.32	5.35	0.27	0.39	5.79	2.55	2.57	2.02	3.03	0.37
04/25/88	44	3.63	0.44	0.36	0.45	0.23	0.35	1.85	0.97	1.92	0.38	5.22	0.48
05/02/88	45	7.21	0.37	0.30	4.90	0.27	0.25	5.61	3.17	5.04	1.46	0.39	0.29
05/09/88	46	0.95	0.19	0.12	6.32	0.30	0.29	5.82	4.65	0.41	2.92	3.25	1.19
05/16/88	47	5.56	7.94	5.59	0.40	0.34	0.34	2.62	1.67	4.73	0.11	0.44	4.11
05/23/88	48	4.19	0.43	0.46	5.50	0.36	0.41	7.72	6.02	0.26	4.35	2.55	0.86
05/30/88	49	3.61	0.44	0.37	0.44	0.28	0.41	1.48	0.24	4.19	0.33	5.84	5.33
06/06/88	50	7.72	1.40	0.32	4.54	0.30	0.36	5.95	4.43	6.77	3.53	0.54	0.20
06/13/88	51	0.22	3.99	0.33	2.51	0.12	0.41	1.59	0.46	1.23	0.39	4.99	4.42
06/20/88	52	3.74	8.59	1.73	1.75	1.06	0.42	5.84	2.57	5.64	1.80	0.34	0.50
06/27/88	53	6.94	0.45	1.07	6.23	5.24	0.49	7.49	4.94	0.48	6.23	6.00	3.18
07/04/88	54	0.02	0.33	0.35	0.45	0.16	0.38		1.01	3.52	0.45	1.54	1.94
07/11/88	55	0.81	0.41	0.20	5.94	0.19	0.13	7.13	3.44	6.05	0.94	6.14	1.39
07/18/88	56												
07/25/88	57												
08/01/88	58	1.88	0.35	3.42	7.00	0.06	0.49	5.32	1.43	0.28	7.00	0.73	1.88
08/08/88	59	0.50	0.38	2.77	0.30	0.16	1.23	0.03	1.75	0.22	0.30	1.66	1.19
08/15/88	60	1.29	0.40	0.39	4.10	0.11	4.36		4.75	0.85	4.10	4.83	1.82
08/22/88	61	5.87	4.64	0.09	1.22	0.03	0.10	0.08	0.03	3.08	0.05	0.10	4.69
08/29/88	62	0.03	2.00	0.01	1.38	1.34	3.01	0.07	1.36	6.14	0.03	0.06	0.22
09/05/88	63							0.04	0.18	0.12	0.02	0.09	0.06
09/12/88	64	2.77	3.56	2.77	0.13	0.03	0.86	0.09	0.05	4.65	0.10	0.12	0.09
09/19/88	65	0.09	0.10	0.31	2.87	0.02	7.55	0.17	0.04	0.10	0.02	0.06	0.03
09/26/88	66							0.11	0.03	1.11	0.08	0.57	0.02
10/03/88	67	0.78	0.12	0.14	0.16	0.16	1.23	0.15	0.03	1.24	0.06	1.02	0.03
10/10/88	68	0.05	0.08	1.87	3.20	0.46	13.74	0.17	0.05	0.44	0.05	6.18	0.06

TABLE 8
Plasma progesterone concentrations (ng/ml)

		GROUP A (12L:12D)						GROUP B (artificial light)					
	sheep	48	49	74	85	189	239	20	39	47	81	93	246
DATE	WEEK												
10/17/88	69												
10/24/88	70												
10/31/88	71								0.06	0.07	0.12	0.05	0.02
11/0 /88	72	0.12	1.69	0.10	0.08	0.03	0.14						
11/14/88	73	0.29	4.98	1.17	3.55	0.03	4.30	0.08	0.06	0.03	0.04	0.98	0.02
11/21/88	74												
11/28/88	75												
12/05/88	76	2.70	4.76	1.42	4.46	0.02	6.05		0.11	0.04	0.07	0.06	0.03
12/12/88	77	2.76	0.17	3.42	0.06	0.96	0.05						
12/19/88	78												
12/26/88	79												
01/02/89	80								0.09	0.11	0.07	0.41	0.03
01/09/89	81												
01/16/89	82	5.26	7.27	5.61	0.12	1.47	0.39						
01/23/89	83	0.05	8.88	0.14	0.14	0.05	3.76						
01/30/89	84							0.17	0.07	0.05	0.08	0.05	0.07
02/06/89	85	0.10	10.96	0.61	0.03	1.15	0.99	0.08	0.06	0.04	0.12	0.06	0.04
02/13/89	86	0.10	0.23	0.07	0.03	0.04	3.21	0.15	0.07	0.02	0.05	0.03	0.02
02/20/89	87							0.16	0.01	0.02	0.04	0.10	0.06
02/27/89	88							0.20	0.16	0.02	0.04	0.16	0.02
03/06/89	89							0.16	0.34	0.02	0.08	2.35	0.03
03/13/89	90	0.05	0.03	0.10	0.02	0.03	0.22	1.04	1.50	0.07	0.03	0.18	0.02
03/20/89	91	0.04	0.15	0.11	0.03	0.04	1.29	2.61	0.03	3.45	0.58	3.18	0.02
03/27/89	92							4.21	1.43	0.12	4.52	0.08	0.05

TABLE 8
Plasma progesterone concentrations (ng/ml)

		-----GROUP C (artificial light)----						------GROUP D (natural light)-				
	sheep	16	54	56	98	107	118	30	31	64	176	202
DATE	WEEK											
06/29/87	1											
07/06/87	2											
07/13/87	3											
07/20/87	4											
07/27/87	5											
08/03/87	6											
08/10/87	7											
08/17/87	8											
08/24/87	9											
08/31/87	10											
09/07/87	11											
09/14/87	12											
09/21/87	13	1.23	0.31	0.02				4.46	0.00	0.05	0.01	0.00
09/28/87	14	1.16	0.20	0.03				1.17	0.54	0.00	0.02	0.00
10/05/87	15	1.16	0.27	0.11				2.20	0.40	0.09	0.00	0.00
10/12/87	16	1.25	0.19	0.06				4.02	4.66	1.98	0.00	0.00
10/19/87	17	1.25	0.20	4.84		0.26	0.34	1.30	0.00	0.04	0.03	0.09
10/26/87	18	1.29	0.20	0.31		0.13	0.34	1.66	4.20	3.67	0.00	3.34
11/02/87	19	1.21	0.15	0.22		0.63	0.20	4.12	0.17	2.95	0.00	0.00
11/09/87	20	1.23	0.21	0.28		0.94	0.19	0.77	3.34	0.28	0.25	2.50
11/16/87	21	1.14	0.06	0.33	0.04	3.38	1.32	2.25	7.54	2.88	0.38	4.88
11/23/87	22	2.08	0.02	1.73	0.00	0.02	0.00	4.76	0.00	0.03	3.75	1.19
11/30/87	23	5.16	0.08	0.79	0.00	0.00	0.01	1.15	******	1.90	0.37	2.63
12/07/87	24	1.06	0.02	0.00	0.00	0.17	6.11	6.69	0.34	3.39	5.84	0.00
12/14/87	25	7.21	0.04	0.00	0.05	3.91	0.44	4.81	0.00	1.69	1.61	4.44
12/21/87	26	1.64	0.04	3.20	4.68	0.11	0.20	3.08	6.32	5.16	0.01	1.92
12/28/87	27	4.99	0.01	3.72	0.08	2.91	6.21	5.87	0.21	1.17	3.66	1.27
01/04/88	28	5.01	0.05	1.70	0.68	5.03	0.06	1.41	5.49	1.77	1.10	5.90
01/11/88	29	3.95	0.04	6.11	5.17	0.87	5.73	7.24	0.18	6.84	4.89	0.00
01/18/88	30	6.28	0.16	0.00	0.23	3.18	0.87	7.09	2.00	0.07	0.00	2.54
01/25/88	31	0.62	0.06	6.16	4.17	0.06	3.14	2.64	6.32	2.07	2.32	0.73
02/01/88	32	5.21	0.11	0.06	0.06	3.69	5.76	6.80	0.00	0.10	0.89	0.00
02/08/88	33	3.18	0.03	0.49	2.74	3.12	0.45	6.53	3.98	0.00	0.00	0.00
02/15/88	34	3.79	0.23	0.55	1.59	0.84	5.40	1.57	0.29	0.06	0.01	0.00
02/22/88	35	7.08	0.00	4.84	2.23	0.32	0.11	7.58	0.00	0.00	0.00	0.00
02/29/88	36	1.11	0.04	0.00	5.41	3.63	3.40	6.23	0.00	0.00	0.07	0.00
03/07/88	37	0.76	0.06	0.00	0.12	4.75	4.31	5.68	0.00	0.00	0.02	0.00
03/14/88	38	1.00	0.09	0.20	1.85	0.25	0.87	5.45	0.00	0.00	0.00	0.00
03/21/88	39	1.07	0.25	0.23	1.60	0.37	7.23	1.23	0.00	0.00	0.07	0.00
03/28/88	40	0.75	0.18	0.35	1.86	0.32	0.20	1.04	0.00	0.00	0.00	0.00
04/04/88	41	0.81	0.07	0.22	1.90	0.26	4.63	0.83				
04/11/88	42	0.88	0.12	0.13		0.21	0.29	0.58				
04/18/88	43	1.15	0.13					0.53				
04/25/88	44	1.53	0.15	0.03	10.15	0.09		0.57				
05/02/88	45	1.06	0.10	0.05	9.69	0.11		0.61	0.03	0.04	0.03	0.02
05/09/88	46	1.17	0.14					0.28				
05/16/88	47	0.78	0.13					0.35				
05/23/88	48	1.12	0.15					0.58				
05/30/88	49	1.14	0.14					0.53				
06/06/88	50	1.23	0.13	0.02	0.95	0.13		0.47				
06/13/88	51	1.13	0.21					0.12				
06/20/88	52	1.23	0.05					0.34	0.02	0.02	0.04	0.02
06/27/88	53	1.24	0.10					0.32				
07/04/88	54		0.20									
07/11/88	55	0.03	0.08	0.04	0.32	0.07		0.03	0.04	0.02	0.02	0.22
07/18/88	56											
07/25/88	57											
08/01/88	58	0.03	0.09	0.07	0.12	0.05		0.02	0.06	0.03	0.03	0.19
08/08/88	59	0.07	0.10	0.07	0.11	0.04						
08/15/88	60	0.07	0.05	0.02	0.13	0.07						
08/22/88	61	0.05		0.05	0.22	0.03		0.03	0.02	0.83	1.27	1.23
08/29/88	62	0.31										
09/05/88	63	0.82	0.06	0.11	0.27	0.04						
09/12/88	64	2.51	0.07	7.68	1.01	0.03		2.49	0.36	2.59	2.81	2.85
09/19/88	65	0.81	0.05	0.12	7.02	0.04		0.04	3.81	0.04	0.43	0.03
09/26/88	66	4.84		0.05	0.08	0.08						
10/03/88	67	[illegible]	0.06	0.05		0.04						
10/10/88	68	[illegible]	0.05	0.15		0.08						

TABLE 8
Plasma progesterone concentrations (ng/ml)

		-----GROUP C (artificial light)----						------GROUP D (natural light)-				
	sheep	16	54	56	98	107	118	30	31	64	176	202
DATE	WEEK											
10/17/88	69							4.90	1.92	2.83	0.22	4.07
10/24/88	'0	1.12	0.09	5.19		0.49		0.56	7.01	0.06	0.35	0.03
10/31/88	71											
11/07/88	72	0.02	0.13	0.48		0.33						
11/14/88	73							0.81	0.28	0.26	0.95	1.17
11/21/88	74	0.21		0.27		0.24		3.64	0.94	2.15	0.04	3.02
11/28/88	75											
12/05/88	76	6.46	0.12	0.22		5.47						
12/12/88	77							4.23	3.09	4.70	0.60	0.05
12/19/88	78	8.35		9.17		4.64		0.07	0.21	0.30	2.50	0.72
12/26/88	79											
01/02/89	80	5.69		11.36		4.46						
01/09/89	81							0.94	0.02	2.80	0.77	2.14
01/16/89	82	4.36	0.12	6.96		0.47		3.17	7.56	2.69	1.44	0.85
01/23/89	83	6.02		0.25		3.14						
01/30/89	84	1.19		7.98		0.15						
02/06/89	85							0.05	4.89	0.08	0.02	0.07
02/13/89	86	0.25	0.09	0.65		0.46						
02/20/89	87			4.74		1.20						
02/27/89	88	2.12										
03/06/89	89	0.08	0.03	5.90		0.08						
03/13/89	90	2.38		2.05		0.04						
03/20/89	91	0.07		0.14		0.02						
03/27/89	92			0.23		0.03						

TABLE 9
weekly food intake (gm)

		GROUP A (12L:12D)						GROUP B (artificial light)				
	SH #	49	48	239	189	74	85	93	20	246	47	81
DATE	WK											
29-Jun-87	1	all sheep given 800 g per day from weeks 1 to 92										
06-Jul-87	2											
13-Jul-87	3											
20-Jul-87	4											
27-Jul-87	5											
03-Aug-87	6											
10-Aug-87	7											
17-Aug-87	8											
24-Aug-87	9											
31-Aug-87	10											
07-Sep-87	11											
14-Sep-87	12											
21-Sep-87	13											
28-Sep-87	14											
05-Oct-87	15											
12-Oct-87	16											
19-Oct-87	17											
26-Oct-87	18											
02-Nov-87	19											
09-Nov-87	20											
16-Nov-87	21											
23-Nov-87	22											
30-Nov-87	23											
07-Dec-87	24											
14-Dec-87	25											
21-Dec-87	26											
28-Dec-87	27											
04-Jan-88	28											
11-Jan-88	29											
18-Jan-88	30											
25-Jan-88	31											
01-Feb-88	32											
08-Feb-88	33											
15-Feb-88	34											
22-Feb-88	35											
29-Feb-88	36											
07-Mar-88	37											
14-Mar-88	38											
21-Mar-88	39											
28-Mar-88	40											
04-Apr-88	41											
11-Apr-88	42											
18-Apr-88	43											
25-Apr-88	44											
02-May-88	45											
09-May-88	46											
16-May-88	47											
23-May-88	48											
30-May-88	49											
06-Jun-88	50											
13-Jun-88	51											
20-Jun-88	52											
27-Jun-88	53											
04-Jul-88	54											
11-Jul-88	55											
18-Jul-88	56											
25-Jul-88	57											
01-Aug-88	58											
08-Aug-88	59											
15-Aug-88	60											
22-Aug-88	61											
29-Aug-88	62											
05-Sep-88	63											
12-Sep-88	64											
19-Sep-88	65											
26-Sep-88	66											
03-Oct-88	67											
10-Oct-88	68											

TABLE 9
weekly food intake (gm)

		GROUP A (12L:12D)						GROUP B (artificial light)				
	SH #	49	48	239	189	74	85	93	20	246	47	81
DATE	WK											
17-Oct-88	69											
24-Oct-88	70											
31-Oct-88	71											
07-Nov-88	72											
14-Nov-88	73											
21-Nov-88	74											
28-Nov-88	75											
05-Dec-88	76											
12-Dec-88	77											
19-Dec-88	78											
26-Dec-88	79											
02-Jan-89	80											
09-Jan-89	81											
16-Jan-89	82											
23-Jan-89	83											
30-Jan-89	84											
06-Feb-89	85											
13-Feb-89	86											
20-Feb-89	87											
27-Feb-89	88											
06-Mar-89	89											
13-Mar-89	90											
20-Mar-89	91											
27-Mar-89	92											
03-Apr-89	93											
10-Apr-89	94											
17-Apr-89	95											
24-Apr-89	96											
01-May-89	97	2452	2521	2985	2985	2985	2881	2812	2986	2059	2976	1316
08-May-89	98	1971	2598	3341	3090	3327	3241	3394	3729	2333	3199	1954
15-May-89	99	2091	2928	3395	2758	3708	3205	3589	3944	3216	3350	1800
22-May-89	100	2264	2995	3300	3280	4015	3436	3244	3271	2964	3477	2033
29-May-89	101	2440	3092	3498	3234	3941	3235	3439	3737	3247	3615	2140
05-Jun-89	102	2360	2832	3204	2886	3708	2859	3316	3813	2903	3076	2272
12-Jun-89	103	2514	2744	3150	2721	3787	3059	3300	3881	2943	3737	2380
19-Jun-89	104	2370	2698	3258	2890	4097	2797	3404	3393	2600	3049	2376
26-Jun-89	105	2458	2755	3395	3090	3934	3090	3154	3616	2300	3657	2464
03-Jul-89	106	2370	2832	3200	3024	3882	2991	3109	3226	2701	3550	2406
10-Jul-89	107	2267	2521	3191	2712	3841	2435	2456	3023	2309	3229	2416
17-Jul-89	108	2265	2764	3168	2504	3585	2594	2666	2886	2433	3544	2491
24-Jul-89	109	2258	2781	2887	2534	3424	2547	2494	3150	2596	3311	2541
31-Jul-89	110	2068	2565	2778	901	3294	2668	3046	3370	2421	3599	2597
07-Aug-89	111	2175	2513	2658	1502	3511	2767	3135	3256	2924	3570	2499
14-Aug-89	112	1908	1941	2148	2241	3097	2610	3001	3367	2820	3153	2469
21-Aug-89	113	2192	2244	2430	3172	3522	2874	2883	2999	3027	3303	2451
28-Aug-89	114	2004	2215	2397	3187	3240	2455	3077	3024	2859	3526	2173
04-Sep-89	115	1678	1670	2380	2925	3358	2351	2850	2897	2819	3367	2244
11-Sep-89	116	503	1937	1750	2874	3070	2287	2750	2714	2604	3569	2300
18-Sep-89	117	367	2037	1865	2567	3094	2558	2956	2974	2866	3148	2343
25-Sep-89	118	883	1734	2626	2857	3244	2854	3111	3239	2941	3413	2536
02-Oct-89	119	1332	1587	2682	2994	2705	2842	3011	3101	2891	3516	2647
09-Oct-89	120	1891	1622	2208	2840	2935	2808	2990	2883	3083	3573	2513
16-Oct-89	121	1532	1894	2507	2797	2730	2642	2741	2757	2947	2949	2497
23-Oct-89	122	1627	1841	2282	2840	2275	2858	2594	2563	3030	3233	2517
30-Oct-89	123	1615	1511	2551	2847	2677	2700	2637	2574	3006	3121	2570
06-Nov-89	124	1502	1754	2432	2811	2522	2698	2597	2547	3119	2843	2480
13-Nov-89	125	1422	2164	2110	2782	2304	2580	2159	2541	3100	3220	2351
20-Nov-89	126	1365	2220	1578	2678	2607	2698	2043	2577	3021	2729	2457
27-Nov-89	127	1528	2307	1360	2625	2192	2402		2887	3153	3157	1619
04-Dec-89	128	1752	2214	1512	2598	2414	2494		2890	3174	2943	927
11-Dec-89	129	1534	2201	1912	2468	2467	2610		2790	3075	2765	1795

TABLE 9
weekly food intake (gm)

		GROUP C (artificial light)				----GROUP D (Natural)---			
	SH #	107	16	54	56	202	30	31	176
DATE	WK								
29-Jun-87	1	all sheep given 800 g per day from weeks 1 to 92							
06-Jul-87	2								
13-Jul-87	3								
20-Jul-87	4								
27-Jul-87	5								
03-Aug-87	6								
10-Aug-87	7								
17-Aug-87	8								
24-Aug-87	9								
31-Aug-87	10								
07-Sep-87	11								
14-Sep-87	12								
21-Sep-87	13								
28-Sep-87	14								
05-Oct-87	15								
12-Oct-87	16								
19-Oct-87	17								
26-Oct-87	18								
02-Nov-87	19								
09-Nov-87	20								
16-Nov-87	21								
23-Nov-87	22								
30-Nov-87	23								
07-Dec-87	24								
14-Dec-87	25								
21-Dec-87	26								
28-Dec-87	27								
04-Jan-88	28								
11-Jan-88	29								
18-Jan-88	30								
25-Jan-88	31								
01-Feb-88	32								
08-Feb-88	33								
15-Feb-88	34								
22-Feb-88	35								
29-Feb-88	36								
07-Mar-88	37								
14-Mar-88	38								
21-Mar-88	39								
28-Mar-88	40								
04-Apr-88	41								
11-Apr-88	42								
18-Apr-88	43								
25-Apr-88	44								
02-May-88	45								
09-May-88	46								
16-May-88	47								
23-May-88	48								
30-May-88	49								
06-Jun-88	50								
13-Jun-88	51								
20-Jun-88	52								
27-Jun-88	53								
04-Jul-88	54								
11-Jul-88	55								
18-Jul-88	56								
25-Jul-88	57								
01-Aug-88	58								
08-Aug-88	59								
15-Aug-88	60								
22-Aug-88	61								
29-Aug-88	62								
05-Sep-88	63								
12-Sep-88	64								
19-Sep-88	65								
26-Sep-88	66								
03-Oct-88	67								
10-Oct-88	68								

17-Oct-88	69								
24-Oct-88	70								
31-Oct-88	71								
07-Nov-88	72								
14-Nov-88	73								
21-Nov-88	74								
28-Nov-88	75								
05-Dec-88	76								
12-Dec-88	77								
19-Dec-88	78								
26-Dec-88	79								
02-Jan-89	80								
09-Jan-89	81								
16-Jan-89	82								
23-Jan-89	83								
30-Jan-89	84								
06-Feb-89	85								
13-Feb-89	86								
20-Feb-89	87								
27-Feb-89	88								
06-Mar-89	89								
13-Mar-89	90								
20-Mar-89	91								
27-Mar-89	92								
03-Apr-89	93								
10-Apr-89	94								
17-Apr-89	95								
24-Apr-89	96								
01-May-89	97	2721	2834	2592	2855	2798	2772	2697	2985
08-May-89	98	3137	3492	3014	3018	3002	2817	2850	3332
15-May-89	99	3510	3854	3320	3301	3245	3394	3061	3367
22-May-89	100	3255	3951	2145	3131	3200	3535	3095	3740
29-May-89	101	3414	3982	3404	2991	3187	3468	3132	3744
05-Jun-89	102	3501	3391	3324	2768	3351	3485	2845	3788
12-Jun-89	103	3552	3412	3517	2950	3478	3590	3374	3907
19-Jun-89	104	3601	3491	3484	3228	3114	3672	3555	4077
26-Jun-89	105	2985	3231	3457	3201	3385	3708	3084	3925
03-Jul-89	106	3618	3192	3184	3194	3517	3620	2728	3797
10-Jul-89	107	3120	3231	3452	2248	2955	3508	2760	4024
17-Jul-89	108	3311	3395	3324	2997	3141	3282	2634	3770
24-Jul-89	109	3315	3194	2977	2631	3081	3405	2567	3931
31-Jul-89	110	3457	3408	3317	2687	2782	3185	2498	3885
07-Aug-89	111	3071	3467	3476	2804	2965	3129	2631	3861
14-Aug-89	112	3435	3184	3335	2851	2848	2918	2494	3708
21-Aug-89	113	3172	3257	3241	2518	2701	3024	2375	3527
28-Aug-89	114	3262	3305	3170	2692	2652	3041	2198	3517
04-Sep-89	115	3208	3200	3017	2270	2338	2814	2008	3385
11-Sep-89	116	3021	2955	2794	2147	2318	2875	2141	3111
18-Sep-89	117	3077	2611	2744	2200	2410	2798	2048	3024
25-Sep-89	118	2405	2790	2917	2542	2414	3160	2255	3401
02-Oct-89	119	3071	2930	3137	2388	2458	2608	2398	3114
09-Oct-89	120	3157	2778	2992	2210	2118	2745	2178	3147
16-Oct-89	121	3047	2704	2930	2130	1701	2807	2302	2345
23-Oct-89	122	2930	2989	2878	2221	2240	2508	1745	2577
30-Oct-89	123	2815	1111	2764	1907	1977	2485	1945	2655
06-Nov-89	124	2771	1850	2475	1941	2384	2264	1922	2321
13-Nov-89	125	2345	2311	2408	2144	2150	2414	1655	2635
20-Nov-89	126	1988	2520	2677	1710	1668	2162	1757	1888
27-Nov-89	127	2441	2220	2632		2051	1812	1004	2018
04-Dec-89	128	2291	2027	1831		1685	1632	1458	1700
11-Dec-89	129	1465	2038			1944	1487	1405	1698

TABLE 10
Percent dry matter digestibilty

		RESTRICTED FEEDING							AD LIBITUM	
	month	SEP 87	DEC 87	APR 88	JUL 88	OCT 88	FEB 89	APR 89	JUN 89	OCT 89
GROUP	SHEEP									
A	48	74.2	75.6	75.8	65.6	73.7	74.5	73.3	47.8	52.2
(12L:12D)	239	75.7	78.2	77.8	72.6	79.4	79.4	78.7	50.4	47.9
	49	75.7	78.3	77.9	72.5	74.3	74.6	76.6	51.4	53.9
	189	73.5	77.5	77.3	72.7	79.4	77.7	73.9	51.4	48.2
	74	73.1	76.5	76.4	75.5	75.3	76.0	71.2	48.4	48.8
	85	74.6	78.2	75.7	67.8	78.1	77.8	72.8	50.5	48.5
B	93	72.8	75.1	76.7	74.7	76.9	77.0	76.6	51.3	49.5
artificial	20	74.3	76.6	76.5	72.0	78.3	77.1	74.4	53.1	48.2
light	246	75.7	79.0	81.3	72.1	81.5	79.9	77.0	48.6	48.5
	81	74.5	77.0	76.6	71.2	76.3	78.6	76.3	44.9	49.4
	47	74.6	75.6	76.5	72.5	79.1	78.8	77.3	50.5	49.0
	39	75.7	75.0	76.2	73.8	78.3	80.6	77.9		
C	107	75.0	78.3	78.3	70.0	72.3	77.0	83.5	48.2	47.2
artificial	16	74.1	77.4	78.5	71.2	75.5	74.8	73.3	53.8	47.2
light	56	74.8	75.6	74.6	71.8	76.4	79.0	73.3	53.9	52.3
	54	75.5	73.4	76.6	71.3	77.2	75.6	71.7	52.1	52.3
	98	75.3	76.8	76.4	68.7					
	118	69.9	75.8	76.9	77.0					
D	176	72.2	75.0	76.8	75.0	77.8	76.8	76.1	44.6	48.6
natural	31	71.2	74.4	73.3	73.9	79.2	75.1	73.6	51.0	47.0
light	30	73.5	73.0	75.5	74.4	77.9	76.0	78.3	47.5	45.9
	64	71.2	76.9	76.7	76.9	78.0	73.5	75.3	47.0	47.2
	202	76.3	74.1	81.2	79.2	82.1	83.7	80.3		
	243	72.5	75.7	79.7	72.5	77.0				