EFFECTS OF SEASON AND PHOTOPERIOD ON GROWTH AND NET FAT SYNTHESIS IN WHITE-TAILED DEER

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ABSTRACT

White-tailed deer (Odocoileus virginianus) in northern ranges are exposed to seasonally hostile climatic conditions. These conditions are most demanding during late winter and early spring. The survival of the deer herd can become uncertain if the winter is prolonged and their physiological preparation for this period is not complete. Accumulation of large fat reserves during the fall is one mechanism used to ensure survival until the following spring. During this period of fat accumulation, white-tailed deer increase their efficiency in converting dietary gross energy to tissue gross energy, which is probably associated with the increased rate of lipogenesis also occurring at this time. Using 15 deer between 9 and 18 months of age, estimated rates of fatty acid synthesis on 19 February, 24 June, and 3 November in the subcutaneous site were 9, 256, and 1515, and for the perirenal site were 1, 245, and 616 nmoles of ^3H_2O/100 mg tissue/2 hr, respectively. High rates of fatty acid synthesis appear to be quantitatively more important than reduced lipolysis in supporting net accumulation of fat. The effects of increased or decreased lipogenic activity were corroborated by the compositional findings of the viscera and skeletal muscle. Ether extract concentrations (dry basis) on 19 February, 24 June and 3 November for viscera were 38.5, 26.2, and 55.1, and for skeletal muscle were 18.4, 13.0, and 37.7%, respectively. Fat and energy concentrations of these

tissues were reduced in late winter to meet energy demands, remained low into early summer, and increased greatly by mid-fall. In another experiment the effects of contrasting (16L:8D vs 8L:16D) photoperiods on net fat synthesis and growth in 19 white-tailed doe fawns from 9 September to 16 December 1981 were examined. Long-day fawns delayed their autumn pelage change, while short-day fawns underwent a normal molt. Short-day fawns were heavier and had accumulated more fat than their long-day counterparts. Short-day fawns also had a higher daily intake of feed, and were more efficient in converting dietary gross energy into tissue gross energy than fawns exposed to the long daylength.

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SECTION I

Effects of Season on Net Fat Synthesis in White-Tailed Does

INTRODUCTION

Seasonal fluctuations in the size of fat depots have been reported in white-tailed deer (Odocoileus virginianus) (Harris 1945) and other wild ungulates (Bear 1971, Anderson et al. 1972, 1974). The amount of stored fat available as a metabolizable energy source during physiologically stressful seasons can influence reproduction, antler growth and, ultimately, the survival of the deer herd (Taber 1958, Verme 1968, 1977).

In late summer or early fall, a change from summer to winter pelage is initiated (Robbins et al. 1974), significantly increasing the insulative qualities of the hair coat (Jacobsen 1980). If food supplies are adequate, fat stores enlarge throughout the fall (Short 1975), with the availability of acorns greatly favoring this accumulation (Duvendeck 1962).

During winter, white-tailed deer demonstrate a behavioral shift which appears to be an energy conserving strategy to ensure survival during this environmentally hostile period. Activity decreases (Ozoga and Verme 1970), less time is spent in the search for food (McMillan et al. 1980), and deer lie in direct sun or under an evergreen overstory in a microclimate that minimizes radiant or convective heat loss (Ozoga 1968). Presumably, the energy expended in seeking food may exceed the energy acquired.

Decreasing body weight and reduced stores of fat characterize the late winter condition, as the amount and quality of available browse declines (Hoffman and Robinson 1966, Ullrey et al. 1970).

The advent of spring brings a lush, nutritious food supply (Dietz et al. 1962, Short et al. 1966), and weight gain follows. However, in pregnant does much of this weight gain is accounted for by the products of conception. At fawning and during lactation, there may be a rather large weight loss once again.

These cyclical patterns of body weight and body fat gain and loss have been linked to the availability of digestible energy supplies (Holter and Hayes 1977). However, Verme and Ozoga (1980) have suggested that net fat synthesis in the fall is an obligatory phenomenon, even during conditions of limited feed intake. If true, either protein accretion must be sacrificed for the accumulation of fat as dietary energy is used for tissue synthesis, or the efficiency with which dietary energy is used for the synthesis of fat must be increased.

In domestic ruminants, fatty acid synthesis takes place in the adipose tissue (as opposed to the liver in nonruminants [Ingle et al. 1972a]), and in vitro techniques have been developed to assess lipogenic (Ingle et al. 1972b, 1973) and lipolytic activity (Metz and Van den Berg 1972, Metz et al. 1973). Using these techniques and changes in body weight and chemical composition, this study was

designed to explore the influence of season on net fat synthesis in white-tailed does from about 9 to 18 months of age.

METHODS

Fifteen female, white-tailed deer born in 1980, were allotted on 14 November 1980 at random from weight outcome groups to 3 groups of 5 deer each at the Houghton Lake Wildlife Research Station and were fed a complete pelleted diet ad libitum (Table 1). This diet supplied approximately 16% protein and 3,000 kcal of digestible energy per kilogram.

Body Composition

Deer were killed in groups of 5 on 19 February, 24 June and 3 November 1981. The deer were weighed, stunned with a captive-bolt pistol, and immediately exsanguinated by incising the carotid and jugular vessels while the deer were suspended by the hind legs. Both the blood and bled carcass were weighed. The deer were then skinned, eviscerated, and the legs removed at the knee (radio-carpal) and hock (tibio-tarsal) joints.

Weights of the skin and tail, head (removed cranial to the atlas, and including covering skin), legs, viscera and carcass (skinned and eviscerated, with head and legs removed) were recorded. The gastrointestinal tract was weighed full and empty. The liver, heart, kidneys and spleen were weighed and, with the empty gastrointestinal tract, were sealed in plastic bags with the remaining

Table 1. Composition of diet fed to white-tailed deer during the study

Ingredient	Percent
Corn cob product[a]	35.0
Soybean meal, 44% crude protein	24.5
Shelled corn	10.0
Wheat middlings	18.0
Alfalfa meal, 17% crude protein	5.0
Cane molasses	5.0
Soybean oil	1.0
Limestone, 38% calcium	0.5
Trace mineral salt	0.5
Vitamin A, D, E and selenium premix	0.3
Mold inhibitor[c]	0.2

[a]Bracts and pith (soft parenchyma without vascular bundles).
[b]Supplied 3,300 IU vitamin A, 220 IU vitamin D, 88 IU vitamin E, 0.2 mg Se (as sodium selenite) per kg of diet.
[c]Mold-Chek®, Flavor Corp. of America Division/Agrimerica, Inc., Northbrook, Ill.

viscera and were refrigerated at 4 C.

The right hind leg was removed from the carcass at the femoral acetabular articulation and was then weighed, boned and the muscle and bone weighed separately. (The right hind leg was processed apart from the rest of the carcass to determine if it might adequately represent total carcass composition.) The remaining carcass was also boned and the muscle and bone weighed. The muscle from the right hind leg and the remainder of the carcass was sealed separately in plastic bags and refrigerated at 4 C.

In the laboratory, the viscera, right hind leg muscle and muscle from the remainder of the carcass were ground 3 times, separately, in a meat grinder (Model 4732-55, Hobart Corp., Troy, Ohio). A 200 g subsample was freeze-dried and ground into a homogeneous mixture in a Waring blender (Model PB-S, Waring Products Corp., New York, N.Y.). Dry matter, crude protein, ether extract, and ash concentrations were determined by AOAC procedures (Horwitz 1980). Gross energy was determined by combustion of samples in an adiabatic oxygen bomb calorimeter (Parr Instrument Co., Moline, Ill.).

Lipogenesis

The rate of fatty acid synthesis was examined by measuring the in vitro incorporation of tritiated water (^3H_2O) into adipose tissue fatty acids, using a modification of the procedure of Ingle et al. (1973). Adipose tissue from the subcutaneous inguinal and perirenal

regions was removed immediately after bleeding and placed in 0.9% saline, maintained at 37 C. Inguinal fat from 3 laboratory mice was used to verify normal assay activity. Tissue slices (100-250 mg) were prepared in triplicate and incubated in flasks with 3 ml of pH 7.4 Krebs-Ringer bicarbonate buffer containing half the usual concentration of $CaCl_2$. This reduced concentration of $CaCl_2$ resulted in more successful distinctions between tissues in their lipogenic activity (pers. commun., D.R. Romsos, Michigan State University, E. Lansing, Mich.). The 3 ml of buffer also contained concentrations of 1.0 unit of bovine insulin/ml and 250 μCi of ^3H_2O/ml, along with 10 mM Na acetate and 5 mM glucose per flask. The tissues were incubated for 2 hours at 90 oscillations per min in a gas mixture of 95% O_2 and 5% CO_2. The reaction was stopped at the end of incubation by transfer of the tissues into glass tubes containing 5 ml of a 30% KOH-methanol (30:70) solution. The samples were then saponified at 50 C in a water bath for 2 hours. Following saponification, the nonsaponified lipids were extracted 3 times with petroleum ether and the extract discarded. The residual aqueous phase was acidified with HCl to approximately pH 2. Again, the samples were extracted 3 times with petroleum ether. The extract was transferred to plastic scintillation vials, dried by evaporation and the residue dissolved in 15 ml of a toluene scintillant (230 ml ethanol, 4 g Omniflour® [New England Nuclear, Boston, Mass.] made to 1 L with toluene).

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Radioactivity was counted by use of a Packard Tri Carb Scintillation Spectrometer (Packard Instrument Co., Downers Grove, Ill.), and quenching was corrected by the channel ratio procedure. The uptake of $^{3}H_2O$ was calculated, and the results were expressed as nanomoles of tritiated water substrate incorporated into fatty acids per 100 mg adipose tissue per 2 hours.

Lipolysis

The rate of lipolysis was determined by measuring glycerol release, in vitro, from adipose tissue. The preparation of tissue slices and incubations were the same as for lipogenesis. However, the tissue slices were incubated in 10 ml of Krebs-Ringer bicarbonate buffer containing concentrations of 5.0% bovine serum albumin and 2 x 10^{-4}M Isoproterenol HCl® (Sigma Chemical Co., St. Louis, Mo). Incubation was terminated by removing the tissue slices from the medium and freezing the remaining medium at -10 C. Prior to glycerol determination, the samples were thawed, and a 1.5 ml aliquot of the remaining medium was placed in a centrifuge tube and deproteinized with 0.3 ml of 30% perchloric acid. After centrifuging for 10 min at 27,000 g, the supernatant was recovered, and glycerol was determined according to Eggstein and Kuhlmann (1974) using a commercial assay kit (Catalog No. 148270, Boehringer Mannheim Biochemicals, Indianapolis, Ind.). Results were expressed as μM of glycerol released per 100 mg tissue per 2 hours.

Weight Gain, Feed and Energy Use

Records of feed intake, live weights, and gross energy concentrations of the diet, skeletal muscle and viscera were used to estimate the efficiency with which air-dry feed or feed gross energy was used for live weight gain or for accumulation of gross energy in body tissues.

Statistical Analyses

Deer were randomly assigned on 14 November 1980 from weight outcome groups to 1 of 3 collection dates (19 Feb, 24 June, 3 Nov 1981). Overall significant differences between collection dates were determined by ANOVA, with $P \leq 0.05$ accepted as significantly different. A Bonferroni t test was used to test for significant differences between 2 means for all combinations. Due to the lower power of the latter test, some parameters exhibited no significant differences between 2 means even through overall significant differences were found. Because of unequal variance in the lipogenic data, the ANOVA was performed on a $\log_{10}$ transformation (Gill 1978).

RESULTS AND DISCUSSION

Body Composition

The mean ($\pm$ SE) liveweight of the 15 doe fawns on 14 November 1980 was 28.5 $\pm$ 0.28 kg with a range of 20.4 to 36.3. Liveweights and weights of the blood, head, skin and tail, legs, gastrointestinal tract and contents, viscera, carcass, skeletal muscle, and bone on 19 February, 24 June and 3 November 1981 were all significantly ($P < 0.05$)

affected by collection date (Table 2). As expected, since these does were in their first year and still growing, all weights increased, with generally greater differences between 24 June and 3 November than between 19 February and 24 June. Liveweights at these sampling times were comparable to those reported by Holter et al. (1977a) for captive white-tailed deer also in their first year.

Blood collected at exsanguination constituted less than 5% of live weight (Table 3). Residual blood still remained in the deer tissues and may have represented up to 50% of the total blood volume, based on studies with cattle (Pearson et al. 1979). The relative proportions of head, legs (removed below the knees and hocks) and bone decreased with time, while the proportions of skin and tail and viscera increased. These latter changes were particularly marked between 24 June and 3 November and appeared to be associated with fat accumulation and the change from summer to winter pelage. Anderson et al. (1971) suggested that mean relative proportions of various body components in mule deer (Odocoileus hemionus hemionus) may reflect significant seasonal fluctuations in body fat rather than actual changes in weight.

The relative proportion of total bone weight of 10.3%, for mule deer, reported by Hakonson and Whicker (1966) is considerably lower than the range of 14.1 to 15.9% found in this study. This can be explained, at least in part, by their adjustment for bone marrow in the long bones. They

Table 2. Weights (kg) of live white-tailed deer and various body components in February, June, and November

Item	19 Feb	24 June	3 Nov	SE	P
No. of deer	5	5	5		
Live weight	30.1[g]	38.9[h]	54.5[i]	2.91	<0.01
Weight after bleeding	28.4[g]	36.8[h]	52.5[i]	2.80	<0.01
Blood[a]	1.4	1.8	2.0	0.15	<0.05
Head[b]	1.6	1.8	2.1	0.07	<0.01
Skin and tail	2.3[g]	2.9[g]	5.4[h]	0.33	<0.01
Legs, below knees & hocks	1.0	1.2	1.4	0.07	<0.01
Gastrointestinal tract, empty[c]	2.2[g]	2.9[g]	4.9[h]	0.39	<0.01
Gastrointestinal contents	2.0[g]	3.1[gh]	4.3[h]	0.40	<0.01
Viscera[d]	3.6[g]	5.0[g]	8.1[h]	0.48	<0.01
Carcass, skinned & eviscerated[e]	17.5[g]	22.2[h]	30.4[i]	1.67	<0.01
Skeletal muscle	12.4[g]	15.9[h]	22.1[i]	1.28	<0.01
Bone[f]	4.8[g]	6.1[g]	7.7[h]	0.41	<0.01

[a]Collected during exsanguination. Probably represents 50% or less of total blood supply (Pearson et al. 1979).
[b]Removed cranial to the atlas. Includes covering skin.
[c]Includes omentum and pancreas.
[d]Includes empty gastrointestinal tract, omentum, pancreas, diaphragm, lungs, trachea, thoracic thymus, liver, spleen, kidneys, ureters, urinary bladder and reproductive system.
[e]Legs removed at knees and hocks. Head removed cranial to the atlas.
[f]Bone remaining after removing skeletal muscle from the carcass. Includes intercostal muscles (which were not removed from the bone).
[ghi]Means within rows with different superscripts are significantly ($P<0.05$) different.

Table 3. Relative proportions (percent of live weight) of various body components of white-tailed deer in February, June, and November

Item	19 Feb	24 June	3 Nov	SE	P
No. of deer	5	5	5		
Weight after bleeding	94.6	94.6	96.2	0.48	NS
Blood[a]	4.6[gh]	4.8[g]	3.6[h]	0.30	<0.03
Head[b]	5.2[g]	4.6[gh]	3.8[h]	0.17	<0.01
Skin and tail	7.7[g]	7.3[g]	10.0[h]	0.27	<0.01
Legs, below knees & hocks	3.2	3.2	2.6	0.10	<0.01
Gastrointestinal tract, empty[c]	7.3	7.4	8.9	0.45	NS
Gastrointestinal contents	6.5	7.8	7.8	0.63	NS
Viscera[d]	11.8[g]	12.8[g]	14.8[h]	0.28	<0.01
Carcass, skinned & eviscerated[e]	58.4	57.1	55.7	0.73	NS
Skeletal muscle	41.3	40.8	40.4	0.86	NS
Bone[f]	15.9[g]	15.8[g]	14.1[h]	0.23	<0.01

[a-f]See footnotes in Table 2.

[ghi]Means within rows with different superscripts are significantly ($P<0.05$) different.

found bone marrow contributed 8.5% to the total bone weight.

Skeletal muscle as a percentage of live weight did not change. Relative skeletal muscle weights for 19 February, 24 June and 3 November were 41.3, 40.8 and 40.4 %, respectively. These values are somewhat smaller than the 46.9% reported by Hakonson and Whicker (1966). Their values ranged from 35.4% for a 22 day old fawn to 52.4% for a 68.2 kg adult male deer, which supported their suggestion that larger deer have a greater proportion of muscle mass than smaller deer. The findings from this study do not support this conclusion. Possibly a relatively large weight difference is needed before this tendency is expressed.

Relative skinned and eviscerated carcass weights were similar for 19 February (58.4%) and 24 June (57.1%), but decreased to 55.7% by 3 November. Contrary to this trend, Verme and Ozoga (1980) found relative carcass weights increased during their fall study of white-tailed fawns fed a high nutritional diet, which was attributed to intermuscular fat storage. They also found food restriction tended to decrease carcass weight as a proportion of total body mass.

The weight of the liver and kidneys increased with time in relation to live weight, and so their relative proportions did not change (Table 4). Robinson (1966) reported weights of various organs for 8 female white-tailed deer ranging from 34 to 66 kg in live weight, but of unknown

Table 4. Weights (g) and relative proportions (percent of live weight) of liver, heart, spleen, and kidneys for white-tailed deer in February, June, and November

Item	19 Feb	24 June	3 Nov	SE	P
No. of deer	5	5	5		
Weights					
Liver	540[a]	759[b]	992[c]	55.4	<0.01
Heart	323	387	417	28.0	NS
Spleen		133	130	13.5	NS
Kidneys	74[a]	103[b]	124[c]	4.3	<0.01
Relative proportions					
Liver	1.80	1.98	1.81	0.060	NS
Heart	1.07	1.01	0.77	0.049	<0.01
Spleen		0.35[a]	0.24[b]	0.028	<0.02
Kidneys	0.24	0.27	0.23	0.014	NS

[abc]Means within rows with different superscripts are significantly ($P<0.05$) different.

age, in December.

The mean liver weight (599.1 g) of Robinson's (1966) deer is similar to the mean liver weight for 19 February (539.6 g) reported here, but smaller than weights on 24 June (759.2 g) and 3 November (991.8 g). Other researchers have provided organ weights for white-tailed fawns fed ad libitum and restricted diets during autumn (Verme and Ozoga 1980). The mean liver weights for fawns on a high diet (ad libitum), moderate diet (2/3 ad libitum), and low diet (1/2 ad libitum) were found to be significantly different between diets. Liver weights for mule deer were heaviest in January the first year of life, but were heaviest in September and October during the second year, and reached their lowest weight in December (Anderson et al. 1974).

The mean kidney (left and right kidney combined) weights for 19 February, 24 June, and 3 November were 73.6, 103.4 and 124.0 g, respectively. Some authors have associated seasonal flucuations in kidney weights with forage quality, voluntary restriction of feed intake, and starvation (Batcheler and Clarke 1970, Anderson et al. 1974). Verme and Ozoga (1980) reported kidney weights of 97.7 g, 76.1 g, and 68.3 g for high, moderate, and low nutritional diets. Other studies have found kidney weights to be highly correlated with body weight (Johns et al. 1980) and dressed weight (Hesselton and Saur 1973) in white-tailed deer. Finger et al. (1981) investigated the relationship between the kidney fat index and the amount of

total body fat in deer and found a relatively high correlation (r^2=0.75).

The weight of the heart increased ($P<0.05$) from 19 February (323.0 g) to 3 November (417.0 g), and was somewhat larger than the mean heart weight of 305.5 g reported for female white-tailed deer in December by Robinson (1966). Seasonal fluctuations in the weight of the heart in deer are influenced by the availability of food (Verme and Ozoga 1980) and, possibly, seasonal changes in metabolic activity (Moen 1978).

In contrast to the data for the liver and kidneys, the relative proportion of heart and spleen decreased with time (although spleens were not collected on 19 February). Robinson (1966) reported heart weights for 8 female white-tailed deer. From these data, the heart as a proportion of total body weight ranged from 0.61 to 0.80% with a mean of 0.70%. Robinson postulated that the heart increased in weight faster than the body during growth. This appears to be contradictory to the findings in the present study since decreasing relative heart weight suggests heart growth is lagging behind that of the body. However, the low relative heart weight for 3 November probably reflects the influence of increased live weight due to autumn fat storage. Hakonson and Whicker (1971) found the mule deer heart comprised 0.85% of the total body mass, while Verme and Ozoga (1980) reported relative heart weights of 0.99%, 0.91%, and 0.95% for high, moderate, and low

nutritional diets, respectively.

It should be noted that differences in organ weights in this study can not be solely attributed to seasonal effects, due to the confounding of growth with season.

The concentrations (% or kcal/g, dry basis) of dry matter, crude protein, ether extract, ash and gross energy in skeletal muscle and viscera of deer were significantly ($P<0.01$) affected by collection date (Table 5). Between 19 February and 24 June, dry matter, ether extract and gross energy concentrations declined and crude protein concentrations increased, consistent with growth and/or further use of body fat for energy. From 24 June to 3 November, muscle and visceral dry matter, ether extract, and gross energy increased remarkably, while crude protein and ash declined. These chemical determinations quantitatively confirmed the presence of large fat reserves observed during necropsy, and it was apparent that this interval included a very significant period of net fat synthesis.

Composition of the right hind leg muscle was determined so comparisons could be made with the composition of the total skeletal muscle. Right hind leg dry matter, ether extract, crude protein, and ash ranged from 24.7 to 29.8%, 9.4 to 24.1%, 67.7 to 83.2%, and 3.6 to 4.4 %, respectively. These components of the right hind leg varied ($P<0.01$) seasonally as did those in the skeletal muscle, but dry matter and ether extract were lower and crude protein and

Table 5. Concentrations (percent or kcal/g, dry basis) of dry matter, crude protein, ether extract, ash, and gross energy in skeletal muscle and viscera of white-tailed deer in February, June, and November

Item	19 Feb	24 June	3 Nov	SE	P
No. of deer	5	5	5		
Skeletal muscle					
Dry matter	28.1[b]	25.2[c]	34.0[d]	0.81	<0.01
Crude protein	70.4[b]	78.5[c]	55.5[d]	2.93	<0.01
Ether extract	18.4[b]	13.0[c]	37.7[d]	2.80	<0.01
Ash	3.9[b]	4.0[b]	2.9[c]	0.21	<0.01
Gross energy	5.68[b]	5.42[b]	6.56[c]	0.139	<0.01
Viscera[a]					
Dry matter	27.6[b]	23.0[c]	34.0[d]	1.47	<0.01
Crude protein	51.4[b]	63.4[c]	37.6[d]	4.00	<0.01
Ether extract	38.5[b]	26.2[c]	55.1[d]	4.19	<0.01
Ash	3.0[bc]	4.0[b]	2.1[c]	0.28	<0.01
Gross energy	6.48[bc]	6.07[b]	7.35[c]	0.213	<0.01

[a]Including empty gastrointestinal tract, omentum, pancreas, diaphragm, lungs, trachea, thymus, liver, spleen, kidneys, ureters, urinary bladder and reproductive system.

[bcd]Means within rows with different superscripts are significantly ($P<0.05$) different.

ash moderately higher. Considering these findings, it is doubtful that the composition of right hind leg muscle can be considered an adequate quantitative index for boned and eviscerated carcass composition, although, similar seasonal fluctuations were exhibited.

Lipogenesis

Based upon in vitro incorporation of ^3H_2O into fatty acids in subcutaneous and perirenal fat, lipogenesis was essentially 0 in February, had increased appreciably by June and was extremely high in November (Table 6). Due to heterogeneous variance of these data, statistical analyses were performed after $\log_{10}$ transformations, with the rate of lipogenesis being significantly ($P<0.02$) affected by date of collection.

Appreciable amounts of fat had been deposited by November which was evident by casual observation during necropsy and was corroborated by the large fat concentrations found by analysis in viscera and skeletal muscle. The high rate of fatty acid synthesis occurring at this time supports the assumption that fat accretion is still occurring at high levels in November. In February it was apparent that a large portion of adipose tissue had been catabolized to meet energy demands. The percentage of body fat was greatly reduced, and there was a drastic decline in the rate of fatty acid synthesis. Fat concentrations were lowest for 23 June, suggesting a further decline in energy reserves into early summer. However, lipogenic activity was

Table 6. Fatty acid synthesis and lipolysis in subcutaneous and perirenal adipose tissue of white-tailed deer in February, June, and November

Item	19 Feb.	24 June	3 Nov	SE	P
No. of deer	5	5	5		
Fatty acid synthesis[a]					
Subcutaneous adipose tissue	9[c]	256[d]	1515[d]	424.5	<0.02
Perirenal adipose tissue	1[c]	245[d]	616[d]	201.5	<0.01
Lipolysis[b]					
Subcutaneous adipose tissue	6	10	7	1.8	NS
Perirenal adipose tissue	7	15	7	1.9	<0.02

[a]In vitro incorporation of ^3H_2O in nmole per 100 mg adipose tissue per 2 hours. Because of heterogeneous variance, the ANOVA was performed on $\log_{10}$ transformed data.

[b]In vitro release of glycerol in μmole per 100 mg adipose tissue per 2 hours.

[cd]Means within rows with different superscripts are signficantly ($P<0.05$) different.

higher in June then February, and it appeared that net fat synthesis was beginning once again. The compositional data reflected the physiological state of the deer manifested over a period of time prior to sampling. In contrast, the procedure employed to quantify lipogenesis only allowed insight into what was occurring during a relatively short time frame. Since information is not available for the period between February and June, energy reserves may have reached their lowest point prior to the June sampling date.

Fatty acid synthesis in ruminant subcutaneous adipose tissue has been shown to adapt to the changing physiological state of the animal. Ingle et al. (1973) observed a 90% reduction in in vitro fatty acid synthesis in lambs deprived of feed for over 60 hours, while fatty acid synthesis increased dramatically within 48 hours of refeeding, reaching a rate not significantly different from the prefasted rate. Deer are known to voluntarily restrict food intake during mid-winter in the wild (Fowler et al. 1967) or in captivity, even when food supplies are adequate (Ozoga and Verme 1970). It would be interesting to establish whether the February decline in in vitro lipogenesis is related somehow to a shortage of substrate in the living animal.

Subcutaneous lipogenic activity was twice that observed for the perirenal site in November. Ingle et al. (1972a) found lipogenic activity to be greatest in subcutaneous sites among adult cattle and sheep, while perirenal and

omental tissue was more active in calves and lambs. Verme and Ozoga (1980) speculated the reason for this might be that, as the animal advances in age, more energy is deposited in subcutaneous fat since less is being used for growth of skeletal and muscle tissue. During periods of fat deposition, internal fat is deposited prior to subcutaneous fat in deer. The reverse order is observed during fat depletion (Harris 1945, Riney 1955). Therefore, the higher subcutaneous rate of lipogenesis observed in November may be a function of the actual time frame of autumn fat deposition, suggesting that, by November, fat accretion has shifted from the perirenal (internal) site to the subcutaneous site.

Lipolysis

As measured by in vitro release of glycerol from subcutaneous and perirenal fat, there was a trend (significant [$P<0.02$] for perirenal fat) for the rate of lipolysis to increase from February to June and to decline again by November (Table 6). However, the magnitude of this change was small, and it would appear that the marked increases in the rate of fatty acid synthesis during the study were quantitatively much more important in supporting the remarkable net synthesis of fat observed between 24 June and 3 November.

Weight Gain, Feed and Energy Use

Live weights on 14 November, 1980 and 19 February, 1981 were nearly the same, with 8 deer gaining weight, 6 deer

losing weight and 1 remaining the same. Average daily feed intake during this period was 1077 g (Table 7), providing about 3231 kcal of digestible energy per day or 262 kcal digestible energy per unit of metabolic body size ($W^{0}_{kg}{}^{.75}$).

From 19 February to 24 June, the does gained about 81 g per day while consuming 1279 g of feed. This provided 275 kcal of digestible energy per $W^{0}_{kg}{}^{.75}$. From 24 June to 3 November, daily gain was 120 g while daily feed was 2182 g or 367 kcal of digestible energy per $W^{0}_{kg}{}^{.75}$.

Based on the grams of gain per grams of feed, the does were slightly less efficient from 24 June to 3 November than from 19 February to 24 June. However, the composition of weight gain during these 2 periods was quite different; at least that was true for the skeletal muscle and viscera. These 2 items, together, constituted 54 to 56% of the live weight. From 19 February to 24 June, the gross energy concentration (wet basis) of skeletal muscle decreased from 1.68 to 1.38 kcal/g, while visceral gross energy concentrations declined from 1.78 to 1.48. From 24 June to 3 November, these values increased to 2.23 and 2.54 kcal/g for skeletal muscle and viscera, respectively. It is probable that the composition of the other tissues, representing 44 to 46% of live weight, changed in the same directions. During the February to June period, an average of 5358 kcal of gross energy were consumed per day. From 24 June to 3 November, the average daily gross energy intake was 9140 kcal, or 1.7 times that in the earlier period.

Table 7. Weight gain, feed and gross energy intake and gain in gross energy in skeletal muscle and viscera in white-tailed deer during various periods from 14 November 1980 to 3 November 1981

Item	19 Feb	24 June	3 Nov
No. of deer	15	10	5
Average live weight, kg	28.5	38.6	54.5
No. of days since last weight	96	125	132
Average daily gain in immediately preceding period, g	0.6	80.6	120.5
Average daily feed in immediately following period, g	1077	1279	2182
Gain/feed x 100	0.1	6.3	5.5
Average GE intake during immediately preceding period, mcal	433	670	1207
Skeletal muscle & viscera, % of live weight	56.1	54.2	55.4
Average GE in skeletal muscle, mcal/kg	1.68	1.38	2.23
Average GE in viscera, mcal/kg	1.78	1.48	2.54
Average GE in muscle & viscera, mcal	27.2	29.3	69.8
Average GE intake per day, kcal	4512	5358	9140
Average gain in GE in muscle & viscera per day, kcal	--	17	307

However, the average daily gains in gross energy in muscle and viscera for the 2 periods were 17 and 307 kcal, respectively, with the latter value being 18.1 times the former.

Some of the difference between February to June and June to November in the efficiency of converting dietary gross energy to tissue gross energy may have been due to greater energy demands for thermoregulation during late winter and spring. The mean ($\pm$ SE) ambient temperature during this period was 6.4 $\pm$ 0.98 C, and ranged from -7.8 to 25.8 C compared to 13.5 $\pm$ 0.57 C, which ranged from -2.2 to 25.3 C from the start of summer to mid-fall. However, the zone of thermoneutrality should be appreciably lower for deer in winter as compared to summer pelage. Thus, the effects of widely different ambient temperatures in winter and summer are modulated to a very significant degree. As a consequence, it is reasonable to assume that a major portion of the greater efficiency with which tissues accumulate gross energy in summer and fall is associated with the accelerated lipogenesis noted in adipose tissue.

SECTION II

Effect of Photoperiod on Growth and Net Fat Synthesis in White-Tailed Doe Fawns

INTRODUCTION

Recently, researchers have become interested in the effects of photoperiod on certain physiological changes that deer undergo annually. Seasonal changes in pelage and feed intake have been linked to changing day length in red deer (Cervus elaphus) (Pollack 1974, Kay and Ryder 1978). White-tailed deer, responding to an extended summer photoperiod, delayed pelage change, while a decrease from a long day (16L:8D) to a short day (8D:16L) stimulated increased growth rates and sexual maturity (Budde 1982). Antler growth cycles also appear to be mediated by photoperiodism (Goss et al. 1969a, 1969b).

Considerable photoperiodic research has been conducted with domestic ruminants, and many of the findings have been contrary to those found with deer. Supplemental light (16L:8D) for sheep significantly increased carcass and slaughter weight (Schanbacker and Crouse 1980). Average daily gain and feed efficiency were also enhanced by exposure to long photoperiod. Experiments with cattle have demonstrated this same increased growth response to supplemental lighting (Peters et al. 1978, 1980).

It is not entirely clear through which physiolgical mechanisms photoperiod has an influence. Many physiological events are under hormonal control. The pineal gland, a

light sensitive organ, may play a role in mediating various hormone levels seasonally, thereby implicating changing day length in circannual endocrine rhythms (Shulte et al. 1981).

In domestic ruminants, serum prolactin concentrations follow a seasonal pattern, with lowest levels occurring during the winter and highest levels during the summer (Koprowski and Tucker 1973, Tucker et al. 1974). Similar seasonal patterns in prolactin levels have been demonstrated in white-tailed deer (Mirarchi et al. 1978, Shulte et al. 1980). Verme and Ozoga (1980) have postulated that lipogenesis is mediated by a decline in prolactin and a rise in adrenocorticotrophic hormone suggesting a possible relationship between decreasing day length (autumn), decreasing prolactin levels and increased lipogenesis.

Since photoperiodic changes can influence seasonal physiological events in white-tailed deer, increased growth and fat deposition triggered by decreasing autumn day length may play a role in the ecological strategy of winter survival in white-tailed deer. If photoperiodism is indeed instrumental in setting the time frame for pelage change, increased fat deposition and energy consumption, then understanding the influence of day length on the timing of these preparatory changes for winter should be useful to wildlife managers.

The objectives of this study were to determine the influence of different photoperiods on the growth and fat metabolism of white-tailed doe fawns as measured by changes

in body composition and the activity of enzymes involved in lipogenesis and lipolysis.

METHODS

Twenty female white-tailed deer fawns were hand-reared in daylight-excluded, indoor pens, and acclimated to a 16L:8D light regime, starting 1 June 1981 at the Rose Lake Wildlife Research Station, East Lansing, Michigan. On approximately 1 August, the fawns were weaned to a pelleted diet provided ad libitum (Table 8). This diet supplied approximately 16.0% protein and 3000 kcal of digestible energy per kg.

On 26 August the fawns were paired according to weight, and randomly split for assignment to 1 of 2 photoperiod treatments. Fawns were weighed weekly, and weekly feed intake per group was monitored. On 9 September the photoperiod treatments began, with 1 pen of deer subjected to 8L:16D (short day), and the other remaining on 16L:8D (long day). These lighting schedules were maintained throughout the study.

Each 4.6 m x 9.7 m pen was equipped with mechanical ventilation and automatic light control systems. A buck (1.5 years old) was housed in an outdoor pen immediately adjacent to the experimental chambers, and ventilation was directed inward to accommodate possible pheromone interaction.

A fawn from the long day pen died on 14 October from unknown causes. It's short day counterpart and 4 randomly

Table 8. Composition of diet fed to white-tailed deer during the study

Ingredient	Percent
Corn cob product[a]	35.0
Soybean meal, 44% crude protein	24.5
Shelled corn	10.0
Wheat middlings	18.0
Alfalfa meal, 17% crude protein	5.0
Cane molasses	5.0
Soybean oil	1.0
Limestone, 38% calcium	0.5
Trace mineral salt	0.5
Vitamin A, D, E and selenium premix	0.3
Mold inhibitor[c]	0.2

[a]Bracts and pith (soft parenchyma without vascular bundles).
[b]Supplied 3,300 IU vitamin A, 220 IU vitamin D, 88 IU vitamin E, 0.2 mg Se (as sodium selenite) per kg of diet.
[c]Mold-Chek®, Flavor Corp. of America Division/Agrimerica, Inc., Northbrook, Ill.

selected pairs were killed on 10 November, with the remaining 10 deer killed on 16 December. Prior to stunning with a captive bolt pistol, a blood sample was taken by jugular venipuncture. The samples were centrifuged at 1500 g for 15 minutes. Blood serum was removed and frozen at -10 C for further analysis. Stunned deer were immediately exsanguinated by incising the carotid and jugular vessels while the deer were suspended by the hind legs. Both bled carcass and blood were weighed. External measurements of body length, shoulder height, chest girth, hind foot length, mandible length, neck circumference, and head length were taken according to Anderson et al. (1974). The deer were then skinned, eviscerated, and the legs were removed at the knee (radio-carpal) and hock (tibio-tarsal) joints. Weights of the skin and tail, head (removed proximal to the atlas, and including covering skin), legs, viscera, and carcass (skinned and eviscerated, with head and legs removed) were recorded. After the entrails were removed, liver, heart, lungs, spleen, uterus, ovaries, kidneys, thyroids, adrenals, thoracic thymus, and full and empty gastrointestinal tract were weighed and sealed in plastic bags with the remaining viscera, and refrigerated at 4 C. The carcass was boned, and both muscle and bone were weighed. The carcass muscle was sealed in plastic bags and refrigerated at 4 C for further analysis.

In the laboratory, a 200 g subsample of liver was taken, and the remaining viscera (including the remaining

liver) and carcass muscle were ground 3 times, separately, in a meat grinder (Model 4732-55, Hobart Corp., Troy, Ohio). A 200 g subsample of viscera, carcass muscle, and liver were separately freeze-dried and ground into homogeneous mixture in a Waring blender (Model PB-5, Waring Products Corp. New York, N.Y.). Dry matter, crude protein, ether extract, and ash concentrations, were determined by AOAC procedures (Horwitz, 1980). Gross energy was determined by combustion of samples in an adiabatic oxygen bomb calorimeter (Parr Instrument Co. Moline, Ill.).

Blood serum was thawed, and used for determination of prolactin levels prior to killing. Prolactin was quantified by double antibody radioimmunoassay (RIA) as previously described by Koprowski and Tucker (1971).

Lipogenesis

The rate of fatty acid synthesis was examined by measuring the in vitro incorporation of tritiated water (^3H_2O) into adipose tissue, using a modification of the procedure of Ingle et al. (1973). Adipose tissue from the subcutaneous inguinal and perirenal regions was removed immediately after bleeding and placed in 0.9% saline, maintained at 37 C. Inguinal fat from 3 laboratory mice was used to verify normal assay activity. Tissue slices (100-250 mg) were prepared in triplicate and incubated in flasks with 3 ml of pH 7.4 Krebs-Ringer bicarbonate buffer containing half the usual concentration of $CaCl_2$. This reduced concentration of $CaCl_2$ resulted in more successful

distinctions between tissues in their lipogenic activity (pers. commun., D.R. Romsos, Michigan State University, E. Lansing, Mich.). The 3 ml of buffer also contained concentrations of 1.0 unit of bovine insulin/ml and 250 μCi of ^3H_2O/ml, along with 10 mM Na acetate and 5 mM glucose per flask. The tissues were incubated for 2 hours at 90 oscillations per min in a gas mixture of 95% O_2 and 5% CO_2. The reaction was stopped at the end of incubation by transfer of the tissues into glass tubes containing 10 ml of a 30% KOH-methanol (30:70) solution. The samples were then saponified at 50 C in a water bath for 2 hours. Following saponification, the nonsaponified substances were extracted 3 times with petroleum ether and the extract discarded. The residual aqueous phase was acidified with HCl to approximately pH 2. Again, the samples were extracted 3 times with petroleum ether. The extract was transferred to plastic scintillation vials, dried by evaporation and the residue dissolved in 15 ml of a toluene scintillant (230 ml ethanol, 4 g Omniflour® [New England Nuclear, Boston, Mass.] made to 1 L with toluene). Radioactivity was counted by use of a Packard Tri Carb Scintillation Spectrometer (Packard Instrument Co., Downers Grove, Ill.), and quenching was corrected by the channel ratio procedure. The uptake of ^3H_2O was calculated, and the results were expressed as nanomoles of radioisotopic substrate incorporated into 100 mg adipose tissue per 2 hours.

Lipolysis

The rate of lipolysis was determined by measuring glycerol release, in vitro, from adipose tissue. The preparation of tissue slices and incubations were the same as for lipogenesis. However, the tissue slices were incubated in 10 ml of Krebs-Ringer bicarbonate buffer containing concentrations of 5.0% bovine serum albumin and 2 x 10^{-4}M Isoproterenol HCl® (Sigma Chemical Co., St. Louis, Mo). Incubation was terminated by removing the tissue slices from the medium and freezing the remaining medium at -10 C. Prior to glycerol determination, the samples were thawed, and a 1.5 ml aliquot of the medium was placed in a centrifuge tube and deproteinized with 0.3 ml of 30% perchloric acid. After centrifuging for 10 min at 27,000 g, the supernatant was recovered, and glycerol was determined according to Eggstein and Kuhlmann (1974) using a commercial assay kit (Catalog No. 148270, Boehringer Mannheim Biochemicals, Indianapolis, Ind.). Results were expressed as μM of glycerol released per 100 mg tissue per 2 hours.

Weight Gain, Feed and Energy Use

Records of feed intake, live weights and gross energy concentrations of the diet, skeletal muscle and viscera were used to estimate the efficiency with which air-dry feed or feed gross energy was used for live weight gain or for accumulation of gross energy in body tissues.

Statistical Analyses

Fawns were paired according to weight on 26 August 1981, and randomly split and assigned to 1 of 2 photoperiod treatments. Similarly, fawn pairs were randomly assigned to 1 of 2 kill dates, either 10 November or 16 December 1981. The statistical procedure used a factorial arrangement of photoperiod and time of kill with the effects of pairs removed, with $P < 0.05$ accepted as significantly different. To determine treatment effects on live weights and average daily gain from 10 November to 16 December, a factorial arrangement of treatment and pairs was utilized.

RESULTS

Weight of Various Body Components

Several body components were substantially heavier in fawns exposed to a shortened photoperiod (Table 9). Weights of the skinned and eviscerated carcass and skeletal muscle were essentially the same for both treatments on 10 November; however, by 16 December the weights of these tissues had increased ($P<.01$) and had diverged between treatment groups. The carcass (18.7 kg) and skeletal muscle (13.5 kg) of short-day fawns were considerably ($P<0.02$) heavier than those of long-day fawns (15.4 kg and 10.6 kg, respectively), and there was a significant ($P<0.01$) treatment x time interaction. Short-day fawns also had a heavier ($P<0.05$) gastrointestinal tract and viscera. Bone weight was not affected by treatment, but did increase over time.

Table 9. Weights (kg) of various body components for white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	K x T[g]
No. of deer	4	5	5	5				
Blood[a]	1.0	0.9	0.9	1.2	0.08	NS	NS	NS
Head[b]	1.2	1.3	1.3	1.5	0.02	<0.01	<0.01	<0.01
Skin and tail	1.7	2.3	2.0	2.8	0.12	<0.02	<0.01	NS
Legs, below knees & hocks	1.0	1.0	1.0	1.0	0.70	NS	NS	NS
Gastrointestinal tract, empty[c]	2.0	2.4	2.1	2.7	0.22	NS	<0.05	NS
Gastrointestinal contents	3.4	3.2	3.6	2.8	0.24	NS	NS	NS
Viscera[d]	3.3	3.8	3.6	4.4	0.27	NS	<0.05	NS
Carcass, skinned & eviscerated[e]	13.8	13.6	15.4	18.7	0.47	<0.01	<0.02	<0.01
Skeletal muscle	9.7	9.7	10.6	13.5	0.38	<0.01	<0.01	<0.01
Bone[f]	3.9	3.8	4.7	5.3	0.18	<0.01	NS	NS

[a]Collected during exsanguination. Probably represents 50 percent or less of total blood supply (Pearson et al. 1979).
[b]Removed cranial to the atlas. Includes covering skin.
[c]Includes omentum and pancreas.
[d]Includes empty gastrointestinal tract, omentum, pancreas, diaphragm, lungs, trachea, thymus, liver, spleen, kidneys, ureters, and urinary bladder. Uterus and ovaries were removed for separate examination.
[e]Legs removed at knees and hocks. Head removed cranial to the atlas.
[f]Bone remaining after removing skeletal muscle from the carcass. Includes intercostal muscles (which were not removed from the bone).
[g]KD = kill date, TRT = photoperiod, K X T = interaction of kill date and photoperiod.

Shortly after 9 September 1981, when treatment photoperiods began, the fawns exposed to the 8L:16D photoperiod initiated their autumn pelage change, while it was delayed in those fawns continued on the 16L:8D regime. This phenomenon was reflected in the heavier skin and tail weights of short-day fawns on both collection dates.

Relative Proportions of Various Body Components

The relative contributions of the skin and tail, to total body mass was larger for short-day fawns on both 10 November and 16 December (Table 10). The relative weight of the gastrointestinal contents decreased with time and was significantly ($P<0.02$) affected by photoperiod, contributing less to the total body weight in short- than in long-day deer. Relative bone weights were not influenced by treatment, but rather, increased ($P<0.02$) with time.

Organs and Glands

Weights of several organs and endocrine glands along with relative proportions of the heart and spleen were affected by treatment and/or time (Table 11). The left kidney of short-day fawns was significantly heavier ($P<0.05$) than the left kidney of their long-day counterparts on both 10 November and 16 December. The left adrenal also displayed a treatment response ($P<0.02$) on 10 November, being heavier in long-day deer. The right adrenal showed this same trend but was not found to be significantly different. The spleen, left kidney, and heart weights all

Table 10. Relative proportions (percent of live weight) of various body components of white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	K x T [g]
No. of deer	4	5	5	5				
Blood[a]	4.0	3.4	3.2	3.6	0.20	NS	NS	NS
Head[b]	4.9	4.8	4.6	4.5	0.11	NS	NS	NS
Skin and tail	6.5	8.6	6.9	8.4	0.26	NS	<0.01	NS
Gastrointestinal tract, empty[c]	7.5	9.1	7.4	8.2	0.68	NS	NS	NS
Gastrointestinal contents	13.4	12.0	12.5	8.4	0.83	<0.04	<0.02	NS
Viscera[d]	12.6	14.4	12.6	13.2	0.73	NS	NS	NS
Carcass, skinned & eviscerated[e]	53.2	50.6	53.6	56.1	1.43	NS	NS	NS
Skeletal muscle	37.4	35.8	37.1	40.3	1.38	NS	NS	NS
Bone[f]	15.4	14.2	16.3	15.8	0.38	<0.02	NS	NS

[abcdefg] Same as Table 9.

Table 11. Weights (g) and relative proportions (percent of live weight) of various organs and glands from white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		10 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	KxT
No. of deer	4	5	5	5				
Liver, g	480	565	566	610	41.4	NS	NS	NS
Liver, % of live weight	1.83	2.14	1.97	1.83	0.014	NS	NS	NS
Heart, g	221	223	296	281	12.8	<0.01	NS	NS
Heart, % of live weight	0.85	0.83	1.03	0.84	0.029	<0.03	<0.01	<0.02
Kidney, right, g	31	35	37	39	1.6	<0.03	NS	NS
Kidney, left, g	30	36	37	39	1.4	<0.01	<0.05	NS
Kidneys (2), % of live weight	0.24	0.27	0.26	0.23	0.010	NS	NS	<0.04
Spleen, g	65	53	76	78	5.7	<0.02	NS	NS
Spleen, % live weight	0.26	0.20	0.26	0.23	0.016	NS	<0.03	NS
Adrenal, right, g	1.1	0.9	1.0	1.0	0.74	NS	NS	NS
Adrenal, left, g	1.3	1.0	1.1	1.1	0.05	NS	<0.02	NS
Lungs, g	340	337	348	325	18.5	NS	NS	NS
Thyroid, right, g	0.8	1.0	1.0	1.1	0.12	NS	NS	NS
Thyroid, left, g	0.9	1.2	1.2	1.1	0.16	NS	NS	NS
Thymus, thoracic, g	10.7	12.3	18.9	14.5	2.81	NS	NS	NS
Uterus, g	9.3	7.0	7.7	14.0	2.00	NS	NS	NS
Ovary, right, g	0.27	0.23	0.29	0.30	0.054	NS	NS	NS
Ovary, left, g	0.28	0.24	0.24	0.27	0.326	NS	NS	NS

increased significantly ($P<0.02$) from 10 November to 16 December. Interestingly, the heart not only exhibited a weight increase over time, but was also equal to or slightly heavier in short- than in long-day fawns on 10 November, with a reversal of this trend by 16 December. Accordingly, the relative contribution of the heart to total body weight in long-day fawns not only was significantly larger ($P<0.01$) than in short-day fawns, but increased ($P<0.03$) by 16 December. The ramifications of these findings will be discussed later. The liver, thoracic thymus, and uterus also appeared to be influenced by treatment and time effects, but no significant differences were found.

External Measurements

Measurements of body length, shoulder height, chest girth, hind foot length, mandible length, neck circumference, and head length all significantly ($P<0.04$) increased with time (Table 12). Only chest girth and neck circumference were influenced by photoperiod ($P<0.01$), being larger in short-day fawns.

Weight Gain, Feed, and Energy Use

Due to pairing according to weight prior to the commencement of the photoperiod treatment on 9 September 1981, the fawns were not significantly different in live weight at the beginning of the study (Table 13). From 9 September to 10 November the deer continued to gain weight ($P<0.01$) with short-day fawns (186 g/day) exhibiting larger average daily gains than long-day fawns (156 g/day). Their

Table 12. Various external measurements[a] (cm) taken from white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	K x T
No. of deer	4	5	5	5				
Body length	107.9	110.0	112.7	118.3	2.06	<0.02	NS	NS
Shoulder height	69.3	68.5	72.1	74.4	1.37	<0.02	NS	NS
Chest girth	61.7	64.7	65.5	74.0	1.19	<0.01	<0.01	NS
Hind foot length	39.4	38.3	40.2	41.8	0.66	<0.02	NS	NS
Mandible length	17.8	17.7	18.0	18.9	0.22	<0.02	NS	NS
Neck circumference	29.3	34.4	34.6	40.1	1.35	<0.01	<0.01	NS
Head length	24.6	24.4	25.2	25.8	0.36	<0.04	NS	NS

[a]Measurements made according to Anderson et al. (1974).

Table 13. Final weights (kg) and average daily gains (g) for white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	KxT
No. of deer	4	5	5	5				
Weight on 26 Aug	14.0	13.8	14.9	14.8	0.29	0.02	NS	NS
Weight on 9 Sept	16.5	15.9	17.5	17.4	0.37	0.02	NS	NS
Final weight	25.8	26.9	28.7	33.4	0.79	<0.01	<0.01	NS
Average daily gain								
9 Sept - 10 Nov	171	201	119	209	14.5	NS	<0.01	NS
9 Sept - 16 Dec			113	161	9.7		<0.03	
10 Nov - 16 Dec			102	102	4.5		NS	

mean final weights for this period were 25.8 kg and 26.9 kg for long- and short-day photoperiods, respectively.

Average daily feed intake for long-day fawns killed on 10 November was 1027 g, providing approximately 3081 kcal of digestible energy per day (Table 14). In comparison, the short-day fawns consumed an average of 1277 g per day, providing approximately 3831 kcal digestible energy. The gain to feed ratio (gain/feed x 100) during this period was 15.6 and 14.8% for long- and short-day fawns, respectively. However, when all 19 fawns were used to calculate this ratio, short-day fawns (15.2%) were more efficient than the long-day fawns (13.0%, Table 15).

The gross energy compositions of the skeletal muscle and viscera, which comprised 47.9% of the live weight in long-day deer and 48.5% in short-day deer, were considerably different by 10 November. The average gross energy concentration in the skeletal muscle in fawns exposed to the 8L:16D photoperiod was 1.81 mcal/kg (fresh basis) as compared to 1.28 mcal/kg for fawns on the 16L:8D photoperiod. The higher gross energy concentrations found in the skeletal muscle of short-day fawns were accompanied by similar elevations in the gross energy concentrations of visceral tissues which were 1.89 mcal/kg and 1.16 mcal/kg for short-day and long-day fawns, respectively.

Those fawns that were killed on 16 December as compared to fawns killed on 10 November, showed similar trends in weight gain during this early period, with even larger

Table 14. Feed and gross energy intake and gain in gross energy in skeletal muscle and viscera in white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December	
	16L:8D	8L:16D	16L:8D	8L:16D
Average daily feed, g				
9 Sept - 10 Nov	1027	1277		
9 Sept - 16 Dec			1135	1424
10 Nov - 16 Dec			1294	1641
Gain/feed x 100				
9 Sept - 10 Nov	15.6	14.8		
9 Sept - 16 Dec			10.0	11.3
10 Nov - 16 Dec			7.9	6.2
Average GE intake, mcal				
9 Sept - 10 Nov	271	337		
9 Sept - 16 Dec			471	591
10 Nov - 16 Dec			195	248
Skeletal muscle and viscera, % of live weight	47.9	48.5	48.4	51.9
Average GE in skeletal muscle, mcal/kg	1.28	1.81	1.44	2.06
Average GE in viscera, mcal/kg	1.16	1.89	1.41	2.30
Average GE in muscle and viscera, mcal	7.52	12.35	10.33	19.05
Average GE intake per day, kcal				
9 Sept - 10 Nov	4303	5351		
9 Sept - 16 Dec			4756	5967
10 Nov - 16 Dec			5422	6876
Average gain in GE in muscle and viscera per day, kcal			66.9	186.1
Gain in GE in skeletal muscle and viscera per GE intake x 100			1.23	2.71

Table 15. Average live weight (kg), average daily gain and feed (g) for all white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	16L:8D	8L:16D
No. of deer	9	10
Average live weight		
26 Aug	14.4	14.3
9 Sept	16.9	16.7
10 Nov	25.3	28.9
Average daily gain		
9 Sept - 10 Nov	134	194
Average daily feed		
9 Sept - 10 Nov	1027	1277
Gain/feed x 100	13.0	15.2

differences in average daily gains and more pronounced divergence in live weight between treatments by 10 November.

During the period from 10 November to 16 December the white-tailed fawns in both treatment groups had an average daily gain of 102 g; however, on 16 December, short-day fawns (33.4 kg) were considerably heavier than their long-day counterparts (28.7 kg). Fawns exposed to the longer daylength consumed less feed (1294 g/day), and had a slightly larger weight gain to feed ratio (7.9%) than did short-day fawns (1641 g/day and 6.2%, respectively). During this period from 10 November to 16 December, long-day fawns had an average daily gross energy intake of 5422 kcal as compared to 6876 kcal for short-day fawns, while the average gains in gross energy per day in muscle and viscera for the 2 treatments were 66.9 kcal and 186.1 kcal, respectively.

Skeletal Muscle and Viscera Composition

Dry matter, crude protein, ether extract, and ash concentrations of the skeletal muscle were significantly affected by time and daylength (Table 16). Percent dry matter was largest ($P<0.01$) in the short-day fawns and increased ($P<0.01$) during the study for both treatment groups. Ether extract concentrations of the skeletal muscle was greatest ($P<0.01$) in the short-day fawns, and increased ($P<0.02$) from 10 November to 16 December. Percent ether extract for long- and short-day fawns on 10 November was 8.1 and 26.4%, respectively, and 12.2 and 33.8% on 16

Table 16. Concentrations (%, dry basis) of dry matter, crude protein, ether extract, and ash in skeletal muscle and viscera in white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	KxT
No. of deer	4	5	5	5				
Skeletal muscle								
Dry matter	25.8	29.9	26.4	32.7	0.47	<0.01	<0.01	NS
Crude protein	84.8	67.7	80.3	60.7	1.29	<0.01	<0.01	NS
Ether extract	8.1	26.4	12.2	33.8	1.83	<0.02	<0.01	NS
Ash	4.4	3.4	4.2	3.0	0.09	<0.03	<0.01	NS
Viscera[a]								
Dry matter	21.8	26.4	23.3	31.8	0.89	<0.01	<0.01	NS
Crude protein	68.1	50.5	64.0	39.9	2.84	<0.05	<0.01	NS
Ether extract	21.5	41.5	29.0	54.0	2.97	<0.02	<0.01	NS
Ash	4.1	3.0	3.5	2.2	0.16	<0.01	<0.01	NS

[a]Including empty gastrointestinal tract, omentum, pancreas, diaphragm, lungs, trachea, thoracic thymus, liver, spleen, kidneys, ureters, and urinary bladder.

December. The higher ether extract values for short-day fawns represents the greater accumulation of fat in this tissue, influenced by the shorter lighting regime. Crude protein and ash concentrations both demonstrated significant treatment ($P<0.01$) and time ($P<0.03$) effects, but showed an inverse relationship to ether extract.

Dry matter, crude protein, ether extract, and ash concentrations of the viscera exhibited similar significant treatment and time effects as did skeletal muscle. Percent ether extract in the viscera for long- and short-day fawns on 10 November was 21.5 and 41.5%, respectively, and 29.0 and 54.0% on 16 December.

Lipogenesis

Lipogenic activity, expressed as the in vitro incorporation of $^{3}H_2O$ into adipose tissue, in both the perirenal and subcutaneous sites of short-day fawns tended to decrease from 10 November to 16 December (Table 17). However, only in subcutaneous adipose tissue was this trend statistically significant. There was also a significant ($P<0.01$) time x treatment interaction for these deer. Perirenal lipogenic activity in long-day fawns was high on both 10 November and 16 December, while subcutaneous lipogenic activity was much lower in comparison.

Lipolysis

As measured by in vitro release of glycerol from subcutaneous and perirenal adipose tissue, there was a significant ($P<0.05$) increase in the rate of lipolysis from

Table 17. Lipogenesis and lipolysis in subcutaneous and perirenal adipose tissue of white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

Item	10 November		16 December		SE	P		
	16L:8D	8L:16D	16L:8D	8L:16D		KD	TRT	KxT
No. of deer	4	5	5	5				
Lipogenesis[a]								
Subcutaneous adipose tissue	187.1	483.3	174.4	69.4	48.57	<0.01	NS	<0.01
Perirenal adipose tissue	568.3	320.4	610.0	113.4	157.80	NS	NS	NS
Lipolysis[b]								
Subcutaneous adipose tissue	9.6	10.0	14.0	12.7	1.30	<0.04	NS	NS
Perirenal adipose tissue	10.3	6.8	14.5	10.7	1.04	<0.01	NS	<0.02

[a]In vitro incorporation of $^{3}H_2O$ in nmole per 100 mg adipose tissue per 2 hours.

[b]In vitro release of glycerol in μmoles per 100 mg adipose tissue per 2 hours.

10 November to 16 December for both treatment groups. Lipolytic activity appeared to be slightly greater in long-day deer, in both fat sites, on 16 December, but the difference was not statistically significant. Perirenal lipolysis also exhibited a time x treatment interaction ($P<0.02$).

Prolactin

Serum prolactin concentrations in long-day fawns were substantially higher than those found in short-day fawns (Table 18). On 10 November the average serum prolactin concentration for long-day fawns was 55.7 ng/ml as compared to 6.8 ng/ml in short-day fawns. On 16 December, the serum prolactin concentrations were 28.5 and 8.1 ng/ml for long- and short-day fawns, respectively.

DISCUSSION

Body Components

During the study, remarkable differences in pelage change in response to differing daylengths were observed. Approximately 4 weeks after the 8L:16D lighting regime was initiated, short-day fawns began to undergo a change from summer to winter pelage. Several long-day fawns also appeared to initiate a change in pelage, but progression of the molt never seemed to pass this preliminary stage. Other long-day fawns maintained their spotted summer coats well into November. However, all short-day fawns underwent a normal molt and were in their winter pelage for the remainder of the study. Similarly, Budde (1983) noted a

Table 18. Concentrations of serum prolactin (ng/ml) in white-tailed fawns exposed to a 16L:8D or 8L:16D photoperiod

	10 November		16 December			P		
Item	16L:8D	8L:16D	16L:8D	8L:16D	SE	KD	TRT	KxT
No. of deer	4	5	5	5				
Prolactin	55.7	6.8	28.5	8.1	7.38	<0.01	<0.12	<0.11

delayed pelage change in white-tailed fawns exposed to a 16 hour daylength as compared to fawns on an 8 hour lighting period which underwent a normal pelage change.

French et al. (1960) were some of the first researchers to report on photoperiodic control of pelage change in white-tailed deer. They reported that changes in spring and fall pelage molts in male white-tailed deer, contrary to this study, were advanced approximately 3 weeks in deer exposed to supplemental light (16 hours) as compared to normal-daylength. The influence of photoperiod on pelage change in roe deer (Capreolus capreolus) (Lincoln and Guinness 1972) and red deer (Kay and Ryder 1978) have also been published. In the latter, not all hair follicles responded in a similar way to a shorter light cycle, thereby suggesting, at least in part, a possible explanation for the partial pelage change in several of the long-day fawns in this study.

The role of contrasting pelage change between treatment groups, with respect to growth and energy use, during a period of decreasing ambient temperatures is significant. As fall progresses and ambient temperatures drop, long-day fawns that retain their summer pelage would eventually expend more energy for thermoregulation than short-day fawns, who have acquired their winter pelage.

The significantly greater carcass, viscera, skeletal muscle, and empty gastrointestinal weights of short-day fawns most likely represent both the greater overall growth,

and the larger accumulations of fat associated with these tissues. Interestingly, the weight of the gastrointestinal contents was smaller in short-day fawns.

Organs and Glands

Photoperiod did not have a profound effect on organ or gland weights. Only the left kidney and left adrenal were significantly different between treatment groups. Whether daylength directly influenced the weight of these organs, or whether these differences were the result of general body growth is unclear. However, it does seem plausible that the adrenal gland enlargement is due to stress in the long-day fawns. The average heart weight, which was the same or slightly greater in short-day fawns on 10 November, was heavier and represented a significantly larger portion of the total body weight in long-day deer by 16 December. If heart rates increase with increased metabolism (Holter et al. 1976, Moen 1978), then perhaps the large relative heart weights observed in the long-day group can be attributed to increased metabolic rate due to cold stress brought on by decreasing ambient temperatures and delayed pelage change.

External Measurements

All external measurements increased over time, which would be expected of growing fawns, while both chest girth and neck circumference were found to be significantly larger in short-day fawns. Anderson (1974) stated that the chest girth measurement is associated with subcutaneous fat depots. Therefore, the greater chest girth measurement of

short-day fawns could be indicative of larger subcutaneous fat deposits in this group. However, it must be noted that the relatively thicker winter pelage of short-day fawns would be reflected in most circumferential measurements compared with fawns in summer pelage. The remaining external measurements were not influenced by daylength. Possibly, the short duration of the study was not great enough to appreciably alter those measurements that are closely related to skeletal growth.

Weight Gain, Feed and Energy Use

The increased rate of gain and heavier final weights of short-day fawns were most certainly influenced by the increased feed intake by this group. Increased feed intake has also been reported during naturally decreasing autumn daylength in free-roaming white-tailed deer (Fowler et al. 1979). Research on red deer has established that dry matter intake is high during artificially decreased daylengths (Pollack 1974, Brown et al. 1979).

The higher efficiency of converting dietary energy into tissue energy of short-day fawns also contributed to the difference in weight gain between each treatment group. Short-day fawns consumed an average of 1.3 times more gross energy per day from 10 November to 16 December than did long-day deer. However, short-day fawns gained an average of 2.8 times more gross energy in muscle and viscera per day than long-day deer. The ratio of gross energy gain in muscle and viscera to gross energy intake for short- and

long-day fawns was 2.7 and 1.2%, respectively. Therefore, it appears likely that both differences in feed intake and the efficiency of utilization of this feed mediated by the photoperiod were responsible for differences in body weight between the treatment groups.

Surprisingly, the average daily gain for both long- and short-day fawns from 10 November to 16 December was 102 g. This rate of gain was lower than the average daily gain for either group in the earlier period. Therefore, not only did the rate of gain decrease during this period, but the effects of contrasting daylength were not expressed in this parameter.

The influence of daylength on the rate of gain and final weights observed in this study have also been documented in lambs (Schanbacher et al. 1982) and cattle (Peters et al 1978). However, long rather than short daylength stimulated increased weight gain in these animals. Forbes et al. (1979a) reported that lambs exposed to 16 hours of light grew significantly faster than short-day lambs (8 hours) on both ad libitum and restricted diets. In cattle, supplemental light (16 hours) also stimulated increased weight gain without increased consumption of feed (Peters et al. 1978), and in both lambs and cattle (Peters et al. 1980), feed conversion ratios favored the long-day treatment.

Skeletal Muscle and Viscera Composition

Considering the compositional findings, short-day fawns

were markedly fatter than the long-day fawns at the end of both periods. At necropsy, considerable differences in gross body fat were evident between the 2 treatment groups. Therefore, it appears that photoperiod mediates fat deposition in white-tailed deer and perhaps other wild ungulates as well. The ecological implications of this condition are obvious. Since daylength influences fat accretion, a particular photoperiodic stimulus (e.g., shortening daylength) may be required before meaningful fat accumulation can take place.

Lipogenesis

Lipogenic activity for both sites in short-day fawns decreased from 10 November to 16 December. Probably fat depots had reached sufficient proportions so that high rates of lipogenesis were no longer necessary. The high rates of fatty acid synthesis in the perirenal site in long-day fawns, in contrast to the modest rates observed in the subcutaneous site, would be indicative of early stages of fat deposition, since internal fat sites are deposited prior to subcutaneous sites (Harris 1945, Riney 1955).

Therefore, short-day fawns were most likely in a final stage of fat deposition by December 16, while long-day fawns were in a more preliminary stage of fat deposition with most lipogenic activity occurring internally and only modest subcutaneous activity.

Surprisingly, the rates of fatty acid synthesis in the perirenal site for long-day fawns on both 10 November and 16

December were comparable to the rate of fatty acid synthesis (616 nmoles of ^3H_2O/100 mg tissue/2 hr) found in this same site for 18 month old white-tailed does exposed to natural daylength in November (Section I). The rate of fatty acid synthesis in short-day fawns was substantially smaller.

The subcutaneous rates of fatty acid synthesis for both groups and periods were considerably lower than the rate of fatty acid synthesis (1515 nmoles of ^3H_2O/100 mg tissue/2 hr) found in this site for the above 18-month old deer in November.

The greater feed intake by fawns exposed to the 8L:16D photoperiod probably promoted lipogenesis. Ingle et al. (1973) observed a 90% decrease in in vitro fatty acid synthesis in lambs deprived of feed for over 60 hours, while fatty acid synthesis increased dramatically by 48 hours after refeeding and reached a rate not significantly different from the prefasted rate.

Lipolysis

The increasing rate of lipolysis from 10 November to 16 December for both treatment groups and fat sites were in the direction one would expect under conditions of decreasing ambient temperature. However, the magnitude of these changes, although significant, was modest at best.

Prolactin

Serum prolactin concentrations were measured to assess the possible relationship between decreasing daylength,

decreasing prolactin levels and increased lipogenesis. Serum prolactin levels were substantially higher in fawns exposed to 16L:8D lighting as compared to fawns under 8L:16D lighting, as would be expected if reduced prolactin levels are associated with net fat synthesis in short-day fawns. Similar research in lambs (Brown et al. 1978, Forbes et al. 1979b, Schanbacher and Crouse 1980, Schanbacher et al. 1982), cattle (Peters et al. 1978), and red deer (Brown et al. 1979) have indicated that prolactin levels are higher when these species are exposed to increased daylength. Bates et al. (1964) reported that prolactin had a fat mobilizing effect in rats. Contrary to this, Meier (1977) reported that exogenous prolactin stimulates marked increases in fat stores in fish, amphibians, reptiles, birds, and mammals within 1 week of daily injections. Other researchers suggest that prolactin levels in white-tailed deer may be related to changes in thyrotropin releasing hormone, and that these changes are mediated by pineal activity (Schulte et al. 1981). Control of serum prolactin levels by thyrotropin releasing hormone has also been reported in cattle (Vines et al. 1977).

CONCLUSION

Wildlife managers have long suspected that seasonal fluctuations in fat play an important role in the survival of the deer herd. Late winter and early spring are often considered the most critical periods of the year, when remaining depots of fat, climatic conditions, and habitat

quality determine the fate of the herd. This thesis has examined the effects of season, and a seasonal phenomenon, daylength, on net fat synthesis in white-tailed deer.

It has been found that fat accumulation and depletion follow seasonal trends that have evolved in relation to dietary energy supplies and in relation to metabolic energy needs. During late summer and fall, deer prepare for winter by accumulating large fat reserves. This is accomplished through increased feed consumption and increased rates of fatty acid synthesis, accompanied by more efficient conversion of dietary gross energy into tissue gross energy. During the winter, deer minimize their energy expenditures through physiological and behavioral modifications, and it is during this period that fat reserves are catabolized. At this time, net fat synthesis is not supportable (because of limited food intake), and fatty acid synthesis is essentially zero. Tissue fat concentrations remain low throughout the spring and early summer, although, fatty acid synthesis in early summer increases. Subsequently, if food supplies are adequate, tissue energy reserves are rebuilt.

In a collateral study, alterations in photoperiod influenced many of the physiological changes that occur seasonally. Deer subjected to shorter days are heavier and accumulate larger fat reserves than deer exposed to longer days. Shortened daylength stimulates increased feed intake

and increases the efficiency with which tissues accumulate gross energy. Long days appear to restrict subcutaneous lipogenic activity with only modest rates of visceral fatty acid synthesis. Therefore, it appears that seasonal fluctuations in tissue fat levels and those factors associated with fat accretion such as energy intake, the efficiency of energy utilization, and net fatty acid synthesis in white-tailed deer (and perhaps other wild ungulates) are mediated by seasonal changes in daylength.

The role of season and photoperiod in regulating the annual physiological rythmns of white-tailed deer should be of considerable interest to wildlife managers. Even though photoperiod is not manipulatable in nature, it is a constraint within which wildlife managers must work. It has been demonstrated that a reduction in daylength can increase fat deposition and energy consumption, and increases the efficiency of tissue energy retention. Thus, seasonal differences in daylength set the time frame for these important physiological events. By coordinating management decisions and habitat manipulations, that provide the energy necessary for fat accretion, within the proper seasonal and photoperiodic time frame, wildlife managers can promote the most appropriate and efficient use of the resources available to deer in preparation for winter.

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