

ENERGY INTAKE IN RELATION TO PUBERTY ATTAINMENT
IN FEMALE BLACK-TAILED DEER FAWNS

by

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Energy intake in relation to puberty attainment in female

black-tailed deer fawns

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Abstract

This project investigated the effect of caloric intake during the fall on the attainment of puberty in female black-tailed deer. The maintenance digestible energy requirement of female fawns in late fall was $173 \text{ kcal/W(kg)}^{.75}/\text{day}$. This is similar to the calculated intake of wild fawns at this time of the year ($153\text{-}183 \text{ kcal./W(kg)}^{.75}/\text{day}$). Five fawns which consumed less than the maintenance requirement of calories failed to conceive, whereas 1 of 2 fawns with a caloric consumption exceeding the maintenance requirement did conceive. Similarly, 22 of 38 female fawns in the experimental herd which consumed high caloric intakes during previous years also conceived. This suggests that fawns must consume a caloric intake in excess of their maintenance requirement for successful conception to occur. Wild fawns are likely unable to obtain a sufficient caloric intake from natural browse plants and thus they do not conceive.

Caloric intake did not appear to affect plasma progesterone levels. Progesterone levels were high in all fawns prior to the breeding season but dropped to low levels in many of the fawns when the breeding season began and they were placed with a buck. This suggests that all fawns may undergo preovulatory cycles which result in elevated progesterone levels. This ovarian activity seems to be inhibited by the onset of the breeding season or the presence of a buck if the fawn is not physiologically prepared to breed. Elevated progesterone values after the breeding season in non-pregnant females make it impossible to

detect pregnancy in deer based on progesterone levels.

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Introduction

Changes in the reproductive rate are extremely important in the regulation of animal numbers. An increase in the reproductive rate can be achieved in 3 different ways: i) decreasing the age at which reproduction first occurs ii) decreasing the interval between subsequent reproductive periods iii) increasing the litter size (Cole 1954). Decreasing the interval between reproductive periods is not a viable alternative in species which occupy seasonally variable environments such as deer (Odocoileus sp.) in temperate regions. Deer in North America breed in the fall and give birth the following spring at about the time when food is most abundant. It is unlikely that fawns born at any other time of the year would be able to survive or to grow to a sufficient size to survive the following winter.

Deer do exhibit some flexibility in litter size. Primiparous females usually give birth to one fawn and subsequently they have one or two fawns depending on their physical condition and nutritional intake (Ransome 1967; Robinette et al. 1973; Verme 1965; Verme 1969). Triplets occur rarely but often they do not survive.

Variation in the age at which reproduction first occurs (puberty) is the most important component affecting the reproductive rate of deer. Female black-tailed deer (Odocoileus hemionus columbianus Richardson) usually breed as yearlings (1½ years) in the wild although some individuals do not breed until 2½ years of age (Brown 1961; Taber 1953). Since about

19-26% of potentially breeding females in a black-tailed deer population are yearlings (Taber and Dasmann 1958), failure of that age class to breed will greatly reduce the productivity of the population. Therefore an understanding of the requirements for puberty in deer is valuable for the management of wild deer populations.

The age at which wild deer first breed is influenced by their nutritional intake which is determined by the quality of the range. Failure of yearling black-tailed does to breed occurs on poor ranges and on extremely poor ranges even 2½ year old does may not breed (Brown 1961; Taber 1953). Similarly, in white-tailed deer (O. virginianus) populations, yearling females are less likely to breed on poor ranges or if they are fed a low-quality diet (Ransome 1967; Verme 1969).

In the wild, 0-58% of female white-tailed deer breed as fawns, depending on the quality of the range (Ransome 1967). Robinette and Gashwiler (1950) reported that 2.2% of 138 yearling mule deer (O.h. hemionus) does were lactating and thus had presumably bred as fawns. However a later study (Robinette et al. 1955) failed to detect any lactating yearlings in a sample of 540 which suggests that in the first study some yearlings may have been aged incorrectly. Brown (1961) examined the reproductive tracts of 65 fawn and 58 yearling black-tailed does in Washington state and found only one individual that showed evidence of breeding as a fawn. Thomas (1970) examined the ovaries of 59 fawn and 116 yearling females from Vancouver Island and found no evidence of breeding in fawns. However

Thomas and Smith (1973) later reported one case of a yearling with a corpus albicantia of pregnancy which indicated that it had bred as a fawn. Therefore, breeding by female black-tailed and mule deer fawns may occur in the wild but it is an extremely rare event.

There are several records of captive, female, black-tailed deer breeding as fawns (Rampont 1926; Shantz 1943; Cowan and Wood 1955) and breeding by female fawns (precocious puberty) has occurred regularly in the captive herd used for the present study. Mueller (1977) observed precocious puberty in 22 of 38 female fawns (58%) over 4 consecutive years. Therefore it is clear that female black-tailed fawns have the genetic potential to breed given the proper conditions but that these conditions are almost never met in the wild.

The most obvious difference between the conditions experienced by captive and wild deer is the quality of their food. Captive deer are usually fed cattle feeds and hay which are far more nutritious than the browse available to wild populations. Mueller (1977) tested the hypothesis that fawns must attain a certain minimal size in order to breed and that wild fawns are unable to reach this size due to their lower nutritive intake. The concept of a critical weight for puberty attainment is based on numerous studies which have shown that the time of puberty in mammals is primarily dependant on achieving a "critical" body weight regardless of age. In rats (Kennedy and Mitra 1963), rabbits (Myers and Poole 1962), cattle (Joubert 1963) and humans (Frisch 1972), puberty occurs at about

the same weight in fast and slow growing individuals but at a significantly greater age in the slow growing individuals.

In seasonally breeding species the critical weight effect is less obvious because animals which attain the critical weight prior to the breeding season cannot yet breed but continue to grow. In domestic sheep, fast growing lambs exhibit first estrus at an earlier date and at a greater weight than slow growing lambs and some slow growing lambs fail to attain puberty at all during their first year (Dyrmundsson 1973). Thus it appears that the slow growing lambs are exhibiting estrus at the minimum necessary body weight and some do not reach this weight during the first breeding season. The fast growing lambs have exceeded the minimum weight before the breeding season commences and they exhibit estrus as soon as the breeding season begins. Therefore in seasonally breeding species, although the effect of a critical weight may not be as apparent as in non-seasonal breeders, non-breeders will still be on average lighter in weight than animals reaching puberty.

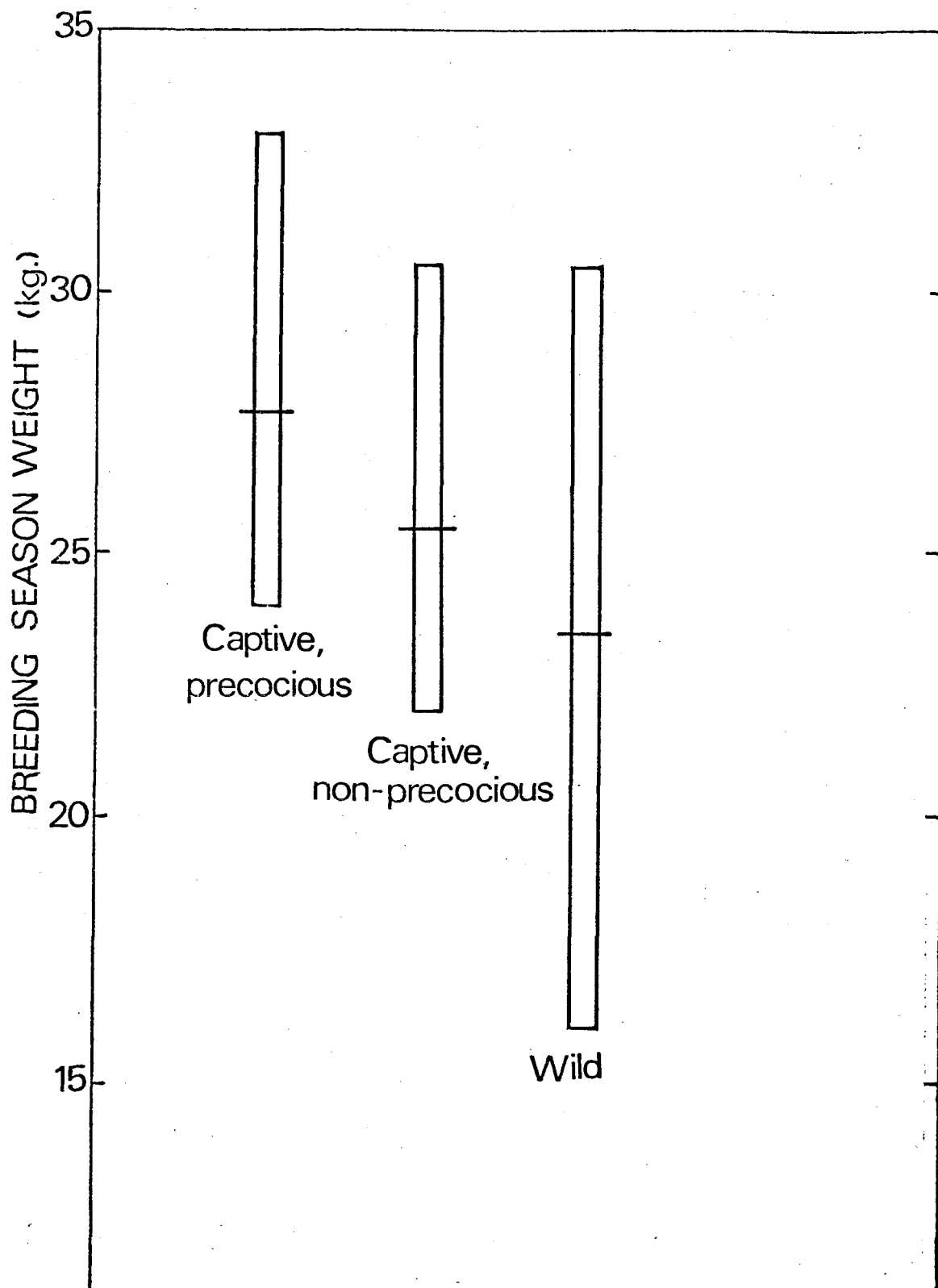
Mueller (1977) found that precocious female fawns were significantly heavier than non-precocious fawns during the breeding season. This indicates that a suitable body weight must be reached before the fawns can breed. However there was a great deal of overlap in the weights of precocious captive fawns at this time, the weights of non-precocious captive fawns and the estimated weights of wild fawns during the breeding season (Figure 1). Many wild fawns reach a size comparable to precocious captive fawns and yet they do not breed. Also, all

wild yearlings exceed the weight of precocious fawns (Mueller 1977) and yet some individuals in this age class do not breed. Therefore some factor other than simply reaching a critical size prevents wild fawns and many yearlings from breeding. The most likely nutritional differences between captive and wild fawns are the protein and energy intakes. This study sought to distinguish which of these nutrients was most important. There is evidence that puberty attainment in other species is influenced by the fat deposits of the female which is related to the caloric intake prior to puberty. Frisch et al. (1973) reported that puberty occurred in human females when an estimated critical body composition of fat as a percentage of body weight was attained. They concluded that a minimum level of fat was necessary for the onset of puberty. In rats, females fed a high-fat diet attained puberty earlier and at a lighter weight than females fed a low-fat diet (Frisch et al. 1977). However, both groups contained identical amounts of body fat at puberty. An experiment by Abler et al. (1976) indicated that puberty in female white-tailed fawns was influenced by caloric intake but not by protein intake. Therefore it seemed likely that puberty attainment in black-tailed deer fawns may also be affected by the caloric intake prior to the breeding season.

Wild deer experience severe nutritional stress during the winter and rely on fat deposits for survival and gestation (Verme 1962; Holl et al. 1979). If a fawn had limited fat deposits it would likely be selectively advantageous not to breed since the fawn would likely be unable to afford the in-

6a.

Figure 1. Comparison of body weights of captive precocious, captive non-precocious and wild black-tailed deer fawns during the breeding season. Data from Mueller (1978).
(Horizontal bar - mean, open block-range)



creased energetic demand for gestation. Natural selection would favour those individuals that did not reach puberty until a suitable amount of body fat was deposited. Captive animals may be able to deposit enough fat for puberty to occur but wild fawns may be unable to deposit enough fat due to a poorer quality nutritive intake and increased energetic demands for activity.

The hypotheses that were tested in this study were:

- 1) Puberty attainment in female black-tailed deer fawns is dependant upon a sufficient caloric intake during the fall.
- 2) Wild fawns are unable to obtain this necessary level of caloric intake from natural browse and thus do not breed.

Methods

Outline of Experiment:

Ten female fawns were weaned in late September of 1977 and raised on either a high energy (H.E.) or a low energy (L.E.) diet. I attempted to detect the onset of puberty by assays of plasma progesterone, observed estrus behavior when placed with a buck, activity level and conception. The caloric value of the experimental diets and natural browse species was determined by in vitro digestion and bomb calorimetry.

Rearing of the Fawns:

The female fawns used in this study came from 2 sources.

i) Nine were born in captivity in the S.F.U. deer enclosure at the U.B.C. Research Forest in Maple Ridge, B.C. during May and June, 1977, to mothers of Vancouver Island stock. Fawns were housed from birth with their mothers in separate outside pens described by Mueller (1977). Eight of the fawns were twins and one was a singleton (2F). The mothers of these fawns were fed ad libitum a 20% protein pelleted cattle feed (Buckerfields Calf-Starter), alfalfa hay and water throughout gestation and lactation. Fresh browse was regularly given in summer. Fawns had ad libitum access to the same feeds during the summer.

ii) Two female fawns (N1, N2) were obtained from the B.C. Fish and Wildlife Branch in Nanaimo, B.C. These fawns had been found in the wild and had been bottle-raised on a powdered milk formula (Dairyade 33, Trimutual Inc.) and fed fresh browse. These 2 fawns were brought to the U.B.C. Research Forest in

mid-August where bottle-feeding of the same formula continued with free access to the pelleted cattle feed and alfalfa.

Weighing Regime:

Fawns were weighed on an electronic platform scale (Western Scale Company). The scale was accurate to 2 grams but fawn weights were rounded to 100 gram accuracy. Weights were taken every 2 weeks from birth until the end of October and then weekly until the end of the experiment in mid-January. Regular weighing of the 2 bottle-raised fawns began in mid-August and subsequently followed the same regime as the mother-raised fawns.

Experimental Regime:

The fawns were weaned on September 26 and placed in individual pens for the experiment. The 11 fawns were randomly allocated to a low energy (L.E.) intake treatment (n=7) or a high energy (H.E.) intake treatment (n=4). A lower number of H.E. fawns was used because many fawns had been raised on H.E. diets during previous years and their conception rate was known (Mueller 1977). Female twins were assigned to opposite treatments. One of the L.E. fawns (N2) died accidentally early in November and was omitted from the analysis of the results.

The H.E. fawns were fed a diet formulated by a commercial feed company (Buckerfields Ltd.) to contain a digestible energy content of 3100 calories/gram and 18% protein (Table 1 & 2) ad libitum. The average daily consumption by weight of these deer was measured each week and converted to intake (g)/W(kg)^{.75}/day because food consumption is related to metabolic weight. The

L.E. deer were restricted to a maximum intake by weight equal to the average intake of the H.E. deer the previous week. The L.E. deer were fed a diet formulated to contain a digestible energy content of 2550 calories/gram and 18% protein (Table 1 & 2). Therefore the L.E. deer were able to obtain as much protein as the H.E. deer but received a reduced caloric intake. Both diets also contained sufficient levels of all other nutrients known to be necessary for ruminants. The average daily intake by weight of the L.E. deer was also measured each week. The food restriction was necessary because deer are known to compensate for decreased digestible energy content of feed by eating more (Ammann et al. 1973).

Fawns were kept in the individual pens at all times until the end of October. From November 1 to December 9 they were released as a group each morning into a large breeding pen with a yearling buck and observed for estrus behavior and copulations for about 4 hours. They were then returned to their individual pens for the remainder of the day. On December 10 the regime was changed in order to maximize the opportunity for breeding. The breeding pen was divided in half to make two breeding pens and a yearling buck was kept in each. The H.E. fawns were kept in one pen and the L.E. fawns were kept in the other pen for 24 hours/day. The fawns were alternated to the other pen each day to eliminate any differences due to the different bucks. The total weight of food consumed by the 4 H.E. fawns was used to compute their average consumption $(g)/W(kg)^{.75}/day$ for each week. An equivalent amount per $W(kg)^{.75}/day$ of the L.E.

Table 1. Composition of Low Energy and High Energy Diets

| | <u>Low Energy Diet</u> | <u>High Energy Diet</u> |
|----------------------|------------------------|-------------------------|
| Mixed Feed Oats | 23.1% | 17.8% |
| Shorts (wheat) | - | 40.0% |
| Soybean Meal (48%) | 5.4% | 2.1% |
| Distillers Grains | - | 7.5% |
| Rape Fines | - | 7.5% |
| Tower Rapeseed Meal | 11.1% | 9.0% |
| Dehydrated Alfalfa | 50.0% | 3.0% |
| Tricalcium Phosphate | - | 0.9% |
| Dicalcium Phosphate | 1.8% | - |
| Limestone | - | 0.9% |
| Molasses | 7.5% | 5.0% |
| Beet Pulp | - | 5.0% |
| Micro-Salt Blend | <u>1.2%</u> | <u>1.2%</u> |
| | 100 | 100 |

Table 2. Manufacturers Analysis of High Energy and Low Energy Diet

| | <u>Low Energy Diet</u> | <u>High Energy Diet</u> |
|--------------------------------------|------------------------|-------------------------|
| Digestible Energy (calories/gram) | 2550 | 3100 |
| Crude Protein (%) | 18.03 | 18.18 |
| Crude Fibre (%) | 15.90 | 9.89 |
| Crude Fat (%) | 2.35 | 5.16 |
| Calcium (%) | 1.26 | 0.88 |
| Phosphorus (%) | 0.69 | 0.74 |
| Salt (%) | 1.0 | 1.0 |
| Total Digestible Nutrients (%) | 57.9 | 70.2 |

feed was fed to the L.E. fawns as a group the following week. Therefore, individual consumptions of the fawns is not known for this period after December 10 but the L.E. group on average was still restricted to an amount equivalent to the average H.E. consumption the previous week.

The experiment ended on January 14 at which time the fawns were separated from the bucks and both groups were placed on an ad libitum diet of the H.E. feed and alfalfa hay for the remainder of the project. The fawns were kept until the end of August, 1978, in order to observe which ones produced fawns.

Bleeding Regime:

Fawns were bled every 2 weeks from the start of the experiment (Sept. 26) until the end of October. From November 3 until January 5 they were bled weekly. The blood sampling was then continued for every 2 weeks until mid-February and then monthly until April. All sampling was done between 10 a.m. and noon. The fawns were immobilized with succinylcholine chloride (Anectine, Burroughs Wellcome Ltd.) injected intramuscularly (0.06mg./kg.). About 10 ml. of blood was taken from the jugular vein using heparinized Vacutainers (Becton, Dickerson & Co.). The blood was centrifuged soon afterwards and plasma was removed and kept frozen until assayed for progesterone.

Activity Measurement:

Activity of the fawns was measured each day between November 1 and December 10 in an attempt to detect estrus. Adult female deer exhibit a dramatic increase in activity on the day of estrus (West 1968). Pedometers (Kasper & Richter Precision

Instruments Ltd.) were attached to neck collars on the deer for the 20 hours/day that they were in the individual pens and read each morning before the fawns were released into the breeding pen. The sexual receptivity of all fawns was also tested at this time each day by pressing on their rump to see if they exhibited lordosis behavior as reported by West (1968).

Pregnancy Detection:

The deer were tranquilized with xylazine (Rompun, Haverlockhart Laboratories) and X-rayed (Easymatic 200, Universal X-ray Products) on March 17 and April 12 to detect the presence of fetal skeletons. This technique has been used successfully to detect pregnancy in deer by Mueller (1977).

Progesterone Assays:

Radioimmunoassays of progesterone were done with 2 different types of commercially available kits. The kit that was originally used was the Biokit (Biolab) but later I switched to the Progesterone (^3H) Radioimmunoassay Pak (New England Nuclear) because it was less expensive and easier to obtain. All assays were done on 0.5 ml. of plasma. The plasma was extracted in solvent but a chromatographic step was not done because numerous investigators have found it to be unnecessary (Runnebaum 1975; Sugden 1978).

The progesterone was extracted from the plasma with diethyl ether for most of the assays but for the final assays petroleum ether was used. There did not appear to be any major differences in the assays due to the kit used or the extraction solvent (Appendix I).

The Biokit assays were done exactly according to the enclosed instructions but the New England Nuclear (N.E.N.) instructions were modified for these assays. In the N.E.N. assays the dried down ether extract was redissolved in 1 ml. of buffer and 0.3 ml. of this solution was assayed in duplicate and 0.3 ml. was counted to determine the recovery rate of the labeled progesterone tracer. The standard curve solutions had their volumes adjusted to allow 0.3 ml. of the standard solutions to be assayed as well.

The standard curve of all assays was calculated as a log-log regression of C.P.M. versus progesterone concentration after Ohman and Fri (1975). The progesterone concentrations of the plasma were calculated from the regression equation. Replicates of the same sample that had a standard deviation greater than 25% of the mean were rejected and the sample was reassayed. Chromotography was done on several samples to determine the effect of cross-reacting steroids. Inter-assay variability and cross-reactivity is discussed in Appendix I.

Food Analysis:

The nutritive value of the L.E. and the H.E. feeds as well as 9 species of natural browse was analysed. Subsamples from 3 different bags of L.E. and H.E. feed were pooled for analysis. The browse samples were collected from the U.B.C. Research Forest on October 12. Only the most succulent parts of the browse plants were collected. The browse species sampled were based on the fall food habits of black-tailed deer reported by Cowan (1945) and Brown (1961).

Dry weight was determined by drying in an oven at 80°C. until a constant weight was maintained. Protein content was determined by measuring the nitrogen content on an HCN analyser (Perkin Elmer Model 240). The percentage protein was calculated as $(6.25) \times (\% \text{ nitrogen})$. The gross energy content of the foods was measured with an adiabatic bomb calorimeter (Gallenkamp CB-110).

The digestibility of the food types was determined by in vitro digestion of 0.5 gram subsamples in triplicate. The in vitro digestion procedure was identical to that reported by Pearson (1970). The rumen fluid was obtained by killing a 20 week old male fawn from the captive herd.

The in vivo digestibility of the L.E. and H.E. feeds was also measured in 2 L.E. and 2 H.E. fawns in mid-December. The 24 hour feces production of these 4 fawns was measured by collecting the feces from the pen. The dry weight of the feces was divided by the dry weight of the average daily food consumption of these animals during the previous 4 days. The caloric value of the L.E. and H.E. feces was determined by bomb calorimetry so that energy digestibility could also be calculated.

Results and Discussion

Nutritional Value of Experimental Diets:

The moisture content of the H.E. and L.E. diets was 13% and 12% respectively. All food consumption values were corrected to represent dry matter intake. The gross energy value of the feeds determined by bomb calorimetry was 4237 calories/gram for the H.E. feed and 4223 calories/gram for the L.E. feed. The caloric value of the feces from the H.E. and L.E. fawns was 4045 calories/gram and 4107 calories/gram respectively.

The in vivo dry matter digestibility of the H.E. feed averaged 74% (73 and 75) and 68% (70 and 66) for the L.E. feed. The energy digestibility of the two feeds was 75% for the H.E. diet and 69% for the L.E. diet. These values were calculated as:

$$\frac{\text{Gross Energy of Feed} - (100 - \text{Dry Matter Digestibility}) (\text{Fecal Energy})}{\text{Gross Energy of Feed}}$$

Since these values are essentially the same as the dry matter digestibility it appears that there is a 1:1 relationship between dry matter digestibility and energy digestibility in deer. Moir (1964) found a similar 1:1 relationship in sheep based on a more extensive investigation.

The in vitro dry matter digestibility was 74.3% for the H.E. diet and 69.4% for the L.E. diet. Since these values are almost identical to the in vivo digestibilities it appears that the in vitro technique provides an accurate estimate of digestibility.

The digestible energy value of the two feeds was calculated by multiplying the gross energy by the digestibility. The digestible energy content was 3185 calories/gram for the H.E. feed and 2909 calories/gram for the L.E. feed. The nutritional value of the feeds is summarized in Table 3.

The feeds had been formulated to contain 3100 calories/gram and 2550 calories/gram based on the digestible energy of the feed constituents in cattle. Deer were more efficient than cattle at digesting the L.E. diet so that the digestible energy of the diets fed to them was greater than anticipated. Palmer et al. (1976) found that in vitro digestibility trials using cow rumen fluid inoculum were equal to those using deer rumen fluid. However, the present findings show that this did not apply in this experiment. Although the difference in the caloric content of the two feeds was not as great as planned, the wide variability in the food consumption between individual deer resulted in a fairly wide range of energy intakes by the experimental animals.

Nutritional Value of Natural Browse:

The gross energy and in vitro dry matter digestibility of 9 of the most commonly browsed plants are presented in Table 4. I have assumed that since there is a 1:1 relationship between energy digestibility and dry matter digestibility for the pelleted diets that this relationship also exists for natural foods. Therefore, the digestible energy of these plants was calculated by multiplying the gross energy by the dry matter digestibility.

Allredge et al. (1974) estimated the food intake of free-

Table 3. Nutritional Analysis of the Experimental Diets

| | <u>Low Energy Diet</u> | <u>High Energy Diet</u> |
|--|------------------------|-------------------------|
| a) Moisture | 12% | 13% |
| b) Gross Energy (calories/gram) | 4223 | 4237 |
| c) Fecal Energy (calories/gram) | 4107 | 4045 |
| d) <u>In vivo</u> Dry Matter | 68% ± 2.8 | 74% ± 1.4 |
| e) <u>In vitro</u> Dry Matter Digestibility | 69% | 75% |
| f) Digestible Energy (e X b) | 2909 | 3185 |
| g) Crude Protein | 21% | 19.6% |

Table 4. Nutritional Analysis of Natural Browse Plants in October

| | Gross Energy (calories/gram) | In vitro digestibility (%) | Digestible Energy (calories/gram) | Crude Protein (%) |
|---|---------------------------------|----------------------------------|---|----------------------|
| Salal (<u>Gaultheria shallon</u>) | 4777 | 32.6 | 1557 | 7.8 |
| Douglas Fir (<u>Pseudotsuga menziesii</u>) | 4988 | 39.3 | 1960 | 11.9 |
| Thimbleberry (<u>Rubus parviflorus</u>) | 4350 | 50.3 | 2188 | 10.9 |
| Salmonberry (<u>Rubus spectabilis</u>) | 4383 | 52.3 | 2292 | 11.6 |
| Willow (<u>Salix spp.</u>) | 5089 | 45.9 | 2336 | 9.5 |
| Red Alder (<u>Alnus rubra</u>) | 4880 | 49.8 | 2430 | 18.1 |
| Vine Maple (<u>Acer circinatum</u>) | 4423 | 56.9 | 2517 | 8.4 |
| Trailing Blackberry (<u>Rubus ursinus</u>) | 4331 | 60.3 | 2612 | 11.9 |
| Red Huckleberry (<u>Vaccinium parvifolium</u>) | 5041 | 54.7 | 2757 | 9.1 |

ranging mule deer from concentrations of fall-out cesium-137 in browse plants and deer tissue. They found that 6 - 11 month old female fawns ate about 32 grams of forage/kg. body weight/day. Therefore, a fawn in the fall which weighed from 25 to 30 kg. would have a daily forage intake of 800 to 960 grams which is equal to about 73 grams/W (kg)^{.75}/day.

Given the daily consumption rate, the proportions of different browse species consumed (Cowan 1945; Brown 1961) and the digestible energy values of these species (Table 4), it is possible to estimate the daily energy intake of an average wild fawn in the fall (Table 5).

The protein intake can be estimated in a similar way based on the protein content of browse species (Table 4). Based on Cowan's (1945) data a fawn would consume 8.4 grams of protein/W(kg)^{.75}/day compared to an intake of 8.2 grams of protein/W(kg)^{.75}/day based on Brown (1961).

Growth of Fawns Before Experiment:

The growth of the mother-raised fawns throughout the summer, prior to the experiment, was normal for the species in captivity. The overall pattern of growth was linear with an average daily weight gain of 0.18 kg. during the first 100 days of life (Figure 2). This is identical to the growth of fawns during previous years at our facility but is slightly lower than weight gains of fawns (0.20 kg/day) reported by Cowan and Wood (1955) for black-tailed fawns over a similar period.

The relative daily growth rate $\frac{W_{t+1} - W_t}{W_t} \times 100\%$

Table 5. Calculation of Caloric Intake from Natural Browse of a Wild Deer Fawn

| Browse Species | Digestible Energy (Calories/gram) | Proportion in Diet | | Amount Eaten** | | Caloric Intake | |
|---------------------|-----------------------------------|-----------------------|--------------------|----------------|------------|----------------|------------|
| | | Van. Is. (Cowan 1945) | Wash. (Brown 1961) | Van. Is. | Wash. | Van. Is. | Wash. |
| Salal | 1557 | 0.27 | 0.05 | 19.7 | 3.7 | 30.7 | 5.7 |
| Douglas Fir | 1960 | 0.08 | 0.01 | 5.8 | 0.7 | 11.4 | 1.4 |
| Thimbleberry | 2188 | 0.06 | 0.00 | 4.4 | 0 | 9.6 | 0 |
| Salmonberry | 2292 | 0.00 | 0.05 | 0 | 3.7 | 0 | 8.4 |
| Willow | 2336 | 0.08 | 0.00 | 5.8 | 0 | 13.6 | 0 |
| Red Alder | 2430 | 0.25 | 0.15 | 18.3 | 11.0 | 44.3 | 26.6 |
| Vine Maple | 2517 | 0.00 | 0.17 | 0 | 12.4 | 0 | 31.2 |
| Trailing Blackberry | 2612 | 0.00 | 0.50 | 0 | 36.5 | 0 | 95.3 |
| Huckleberry | 2757 | 0.00 | 0.05 | 0 | 3.7 | 0 | 10.1 |
| Other | <u>2294*</u> | <u>0.26</u> | <u>0.02</u> | <u>19.0</u> | <u>1.5</u> | <u>43.5</u> | <u>3.3</u> |
| TOTAL | | 1.00 | 1.00 | 73.0 | 73.2 | 153.1 | 182.0 |

* mean value of analysed browse species

** assuming daily consumption = 73 grams/W(kg)·75

of the mother-raised fawns decreased during the first 100 days of life. The daily growth rate was highest between 10 and 20 days of age and then gradually decreased between the ages of 20 to 100 days of age (Table 6). The rapid initial relative daily growth rate corresponds to Cowan and Wood's (1955) phase II growth and the subsequent decreasing rate corresponds to phase III growth. A very rapid phase I growth can occur before 10 days of age but it is highly variable and often does not occur (Cowan and Wood 1955). Insufficient weight data were collected during the first 10 days to determine whether or not phase I growth occurred in the present study.

The daily growth rate of 4.6% between 10 and 20 days is comparable to the rate of 5% observed by Cowan and Wood (1955) in black-tailed fawns during phase II, 5.5% during the first 12 days in mule deer fawns (Robinette et al. 1973) and 3% for white-tailed fawns during the first 28 days (Verme 1963). The declining growth rate from 1.8% to 1.2% between 20 and 90 days is close to the 1.1% to 1.5% daily growth observed by Cowan and Wood (1955) in black-tailed fawns during phase III and the 1.7% growth rate between 13 and 75 days in mule deer fawns (Robinette et al. 1973).

The bottle-raised fawn (N1) grew much more slowly with an average daily weight gain of about 0.11 kg. prior to the experiment. Therefore, at the start of the experiment this fawn was the smallest individual even though it was the oldest.

The average weight of the fawns at the beginning of the experiment was 21.2 ± 2.7 kg. excluding the stunted fawn and

24a.

Figure 2. Weight growth of mother-raised fawns for first 100 days.

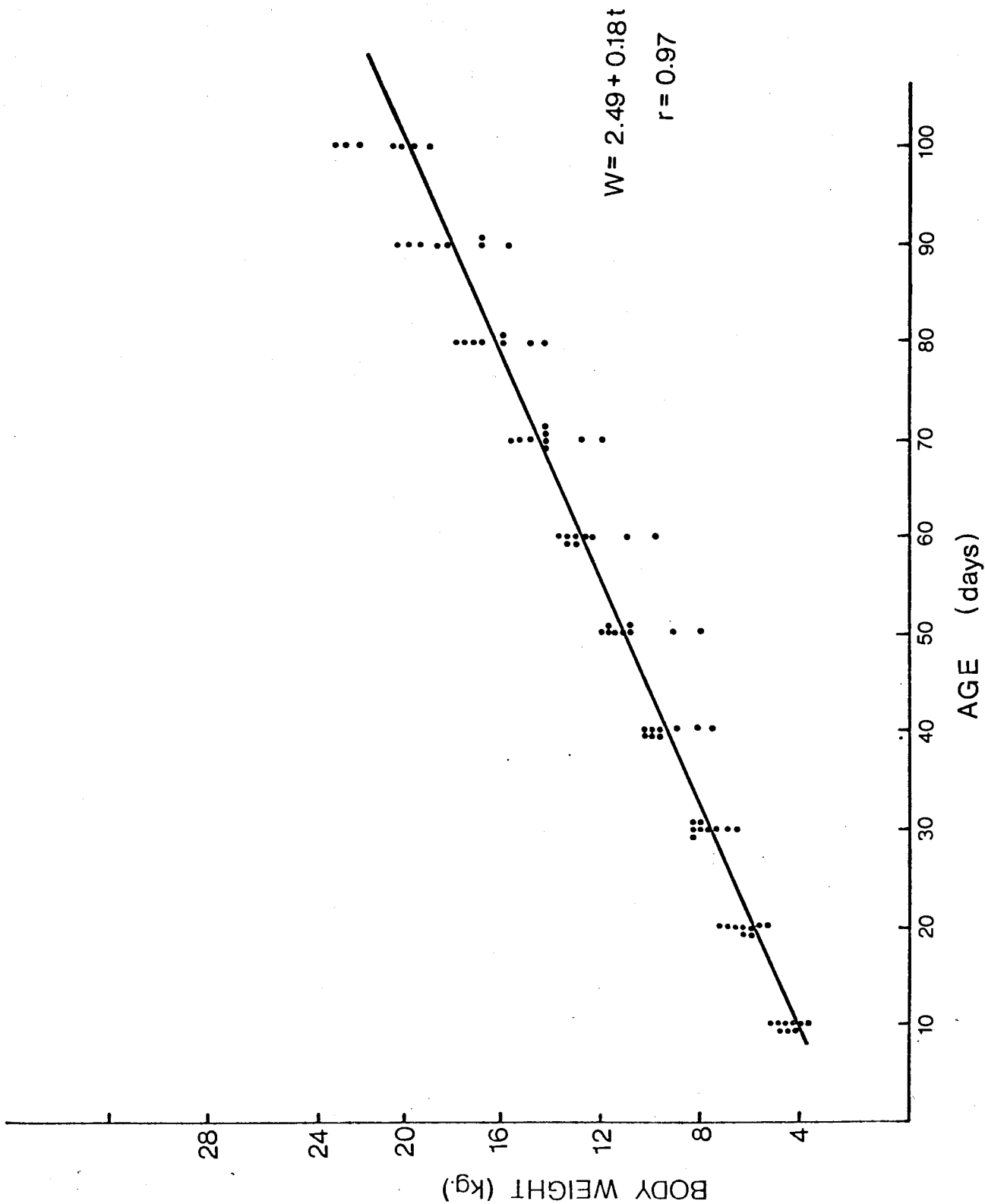


Table 6. Relative Daily Growth Rates of Fawns for First 90 Days

| <u>Age (days)</u> | <u>Relative Daily Growth Rate (%)</u> |
|-------------------|---|
| 10-20 | 4.6 |
| 20-30 | 1.8 |
| 30-40 | 2.2 |
| 40-50 | 1.7 |
| 50-60 | 1.6 |
| 60-70 | 1.5 |
| 70-80 | 1.3 |
| 80-90 | 1.2 |

ranged from 17 - 23.8 kg. The stunted fawn weighed 16.2 kg. All fawns were within the normal weight range for their particular age at this time (Mueller and Sadleir 1980) except for the bottle-raised fawn. Overall, the fawns used in this experiment exhibited normal growth for this species in captivity but differences in age and individual growth rate resulted in a substantial range of weights at the beginning of the experiment.

Growth of Fawns During Experiment:

The weights of the fawns placed in the H.E. and L.E. treatments were:

| | <u>N</u> | <u>\bar{X}</u> | <u>Range</u> |
|------|----------|-----------------------------|-----------------|
| H.E. | 4 | 20.9 | 16.2 - 23.8 kg. |
| L.E. | 6 | 20.7 | 17.0 - 23.6 kg. |

The H.E. fawns continued to grow during the first 4 weeks of the experiment but their daily weight gain and growth rate decreased over this period (Table 7A-B). "The point when daily weight gains begin to decrease" was the definition of the "inflection point" of growth used by Bandy (1955). The inflection point of the H.E. fawns occurred about mid-October. Growth of the H.E. fawns simultaneously stopped or dramatically slowed about October 31. This date was the mid-point of the first 2 week weighing period in which the weight gain was less than 1 kg. Cowan and Wood (1955) describe a growth halt in male fawns which they call the pubertal break. However this halt occurred in different fawns over a range of several weeks and thus may not be directly comparable to the sudden, synchronous growth halt observed in this experiment. The growth halt can also be iden-

Table 7A. Average Daily Weight Gain of Fawns During the Fall

| Date | Fawn # | H.E. Fawns | | | | $\bar{X} \pm$ | S.D. |
|-------------------------|--------|---------------|---------------|---------------|---------------|---------------|------|
| | | 22G | 16G | EE | N1 | | |
| Sep 26 - Oct 10 | | 0.21 (kg.) | 0.15 (kg.) | 0.24 (kg.) | 0.24 (kg.) | 0.21 \pm | .04 |
| Oct 10 - 24 | | 0.13 | 0.06 | 0.16 | 0.13 | 0.12 \pm | .04 |
| ————— growth halt ————— | | | | | | | |
| Oct 24 - Nov 10 | | 0.02 | 0.00 | 0.04 | 0.02 | 0.02 \pm | .02 |
| Nov 10 - 24 | | 0.12 | 0.05 | 0.03 | 0.04 | 0.06 \pm | .04 |
| Nov 24 - Dec 8 | | 0.06 | 0.00 | 0.09 | 0.06 | 0.05 \pm | .04 |
| Dec 8 - 22 | | -0.06 | 0.00 | 0.04 | 0.00 | -0.01 \pm | .04 |
| Dec 22 - Jan 5 | | 0.03 | -0.02 | 0.02 | 0.04 | 0.02 \pm | .02 |

| Date | Fawn # | L.E. Fawns | | | | | $\bar{X} \pm$ | S.D. | |
|-------------------------|--------|------------|-------|-------|-------|-------|---------------|---------------------|-----|
| | | 22F | 30E | OBE | 16F | ED | | | 2F |
| Sep 26 - Oct 10 | | 0.22 | 0.15 | 0.22 | 0.21 | 0.17 | 0.18 | 0.19 \pm (kg.) | .03 |
| Oct 10 - 24 | | 0.08 | 0.09 | 0.09 | 0.09 | 0.03 | 0.06 | 0.07 \pm | .02 |
| Oct 24 - Nov 10 | | 0.08 | 0.09 | 0.08 | 0.15 | 0.14 | 0.16 | 0.12 \pm | .04 |
| ————— growth halt ————— | | | | | | | | | |
| Nov 10 - 24 | | -0.05 | 0.03 | -0.01 | -0.06 | -0.06 | -0.04 | -0.03 \pm | .03 |
| Nov 24 - Dec 8 | | 0.00 | -0.01 | 0.02 | 0.01 | 0.00 | -0.04 | 0.00 \pm | .02 |
| Dec 8 - 22 | | -0.02 | 0.05 | -0.04 | -0.06 | 0.05 | 0.00 | 0.00 \pm | .04 |
| Dec 22 - Jan 5 | | 0.06 | 0.08 | 0.07 | 0.04 | 0.11 | 0.14 | 0.08 \pm | .04 |

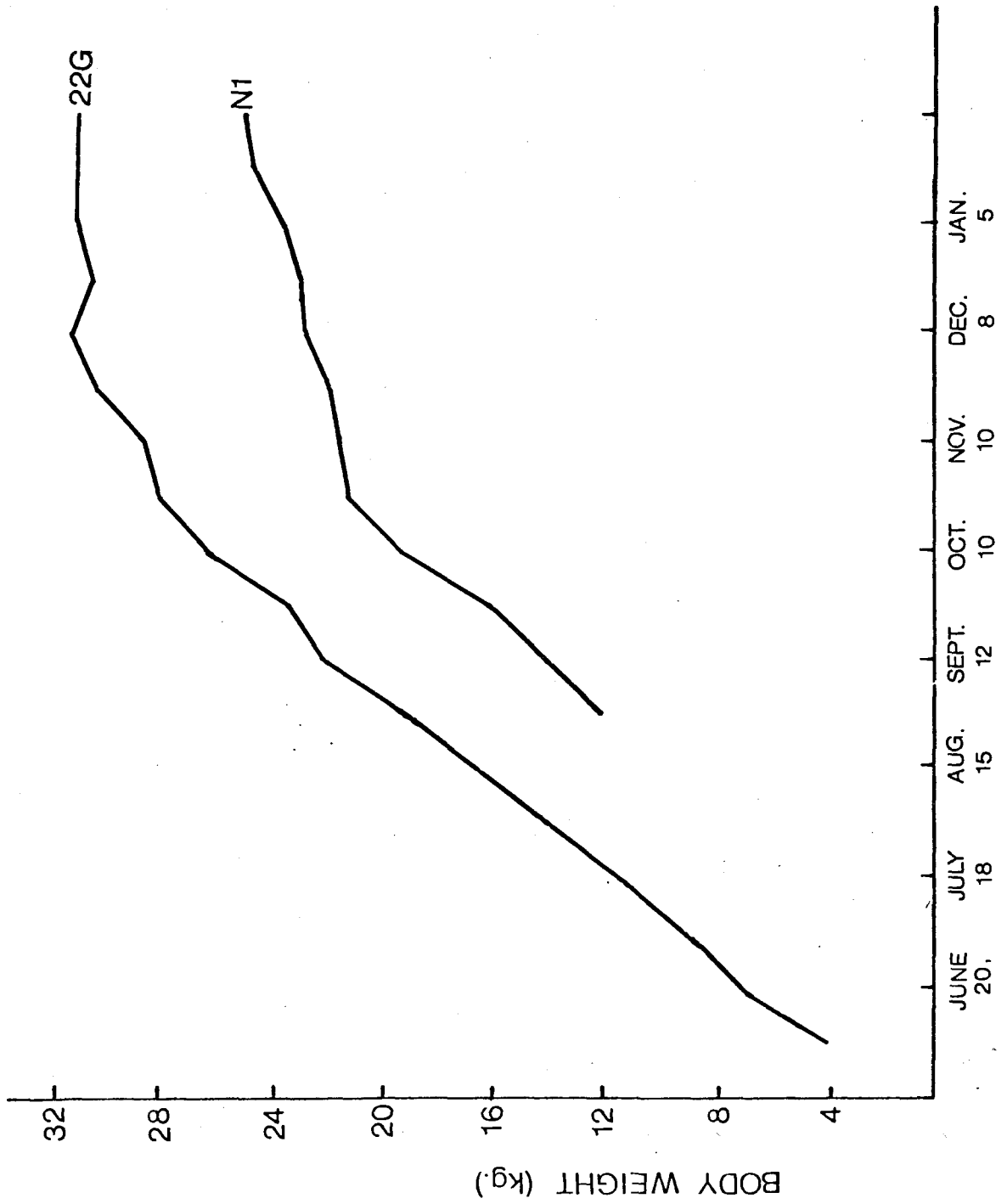
Table 7B. Daily Growth Rate (%) of Fawns During the Fall

| Date | Fawn # | H.E. Fawns | | | | \bar{X} | S.D. |
|-----------------|--------|------------|-------|------|------|-----------|------------------|
| | | 22G | 16G | EE | N1 | | |
| Sep 26 - Oct 10 | | 0.87 | 0.68 | 1.33 | 1.46 | 1.09 | ⁺ .37 |
| Oct 10 - 24 | | 0.48 | 0.27 | 0.73 | 0.66 | 0.54 | ⁺ .21 |
| growth halt | | | | | | | |
| Oct 24 - Nov 10 | | 0.10 | 0.00 | 0.15 | 0.08 | 0.08 | ⁺ .06 |
| Nov 10 - 24 | | 0.42 | 0.20 | 0.12 | 0.20 | 0.24 | ⁺ .13 |
| Nov 24 - Dec 8 | | 0.21 | -0.03 | 0.35 | 0.26 | 0.20 | ⁺ .16 |
| Dec 8 - 22 | | -0.18 | -0.03 | 0.14 | 0.00 | -0.02 | ⁺ .13 |
| Dec 22 - Jan 5 | | 0.09 | -0.08 | 0.08 | 0.19 | 0.07 | ⁺ .11 |

| Date | Fawn # | L.E. Fawns | | | | | \bar{X} | S.D. | |
|-----------------|--------|------------|-------|-------|-------|-------|-----------|-------|------------------|
| | | 22F | 30E | OBE | 16F | ED | | | 2F |
| Sep 26 - Oct 10 | | 0.97 | 0.65 | 0.98 | 0.88 | 1.01 | 1.00 | 0.92 | ⁺ .14 |
| Oct 10 - 24 | | 0.30 | 0.37 | 0.33 | 0.32 | 0.15 | 0.32 | 0.30 | ⁺ .08 |
| Oct 24 - Nov 10 | | 0.29 | 0.29 | 0.24 | 0.45 | 0.59 | 0.61 | 0.41 | ⁺ .16 |
| growth halt | | | | | | | | | |
| Nov 10 - 24 | | -0.15 | -0.10 | -0.03 | -0.22 | -0.26 | -0.18 | -0.16 | ⁺ .08 |
| Nov 24 - Dec 8 | | 0.03 | -0.05 | 0.08 | 0.05 | 0.00 | -0.19 | -0.01 | ⁺ .10 |
| Dec 8 - 22 | | -0.08 | 0.21 | -0.15 | -0.20 | 0.24 | -0.03 | 0.00 | ⁺ .19 |
| Dec 22 - Jan 5 | | 0.29 | 0.28 | 0.26 | 0.13 | 0.53 | 0.61 | 0.35 | ⁺ .18 |

29a.

Figure 3. Body weight growth curves of the largest and smallest H.E. fawns.



tified in the individual growth curves of the fawns as a sudden flattening of the curve (Figure 3) and the timing of the halt corresponds to a dramatic voluntary reduction of feed intake which will be discussed below.

The timing of the growth halt appears to be a seasonal rather than an age or size-dependant effect since it occurred in all the H.E. fawns during the last week of October over a range of ages from 120 to 147 days and a range of weights from 21.3 to 28.5 kg.

The growth rate of the H.E. fawns after the growth halt was essentially zero with occasional weight losses and no bi-weekly gains exceeding 1 kg. for the remainder of the experiment. The average daily weight gain during this period was $0.2 \pm .02$ kg.

The L.E. fawns also continued to grow rapidly during the first part of the experiment (Table 7A-B). However both the daily weight gain and the growth rates were less than that observed in the H.E. fawns. Therefore the reduced energy intake during this period caused a reduction in growth. The L.E. fawns also exhibited a growth halt but it occurred about 2 weeks later than in the H.E. fawns. This may have been due to these fawns being restricted to a reduced food intake at this time which corresponded to the low intake of the H.E. fawns during their growth halt. It is not clear if the L.E. fawns would have stopped growing even if their food intake had not been restricted. However, the same week that the H.E. fawns decreased their food intake, all but one of the L.E. fawns ate

only 80 - 90% of their ration. This suggests that they were voluntarily decreasing their intake at the same time and may also have stopped growing.

Wood et al. (1962) found that slow-growing buck fawns on a 70% plane of nutrition failed to exhibit a growth halt and continued to grow whereas high-plane fawns stopped growing at 5 months of age. Nordan et al. (1968) found that male fawns raised on a low plane of nutrition did not exhibit a voluntary decrease in food intake and weight gains comparable to high-plane males. They suggested that the low-plane animals do not have sufficient fat reserves to allow them to stop eating. The female fawns studied by Nordan et al. (1970) did not exhibit a growth halt but these fawns had been bottle-raised and were exceptionally small (17 kg.) at the end of October. Overall, it appears that a normally growing fawn will dramatically decrease its food intake and stop growing about the end of October. However an undernourished fawn will continue eating and growing to compensate for its poorer condition. Since the growth halt was not size dependant but was delayed by an energy reduction, the signal for the growth halt may be the fat deposits of the animal.

The growth of the L.E. fawns after the growth halt fluctuated around zero with some small gains and losses (Table 7A-B). The average daily weight gain was $0.01 \pm .05$ kg. during this period.

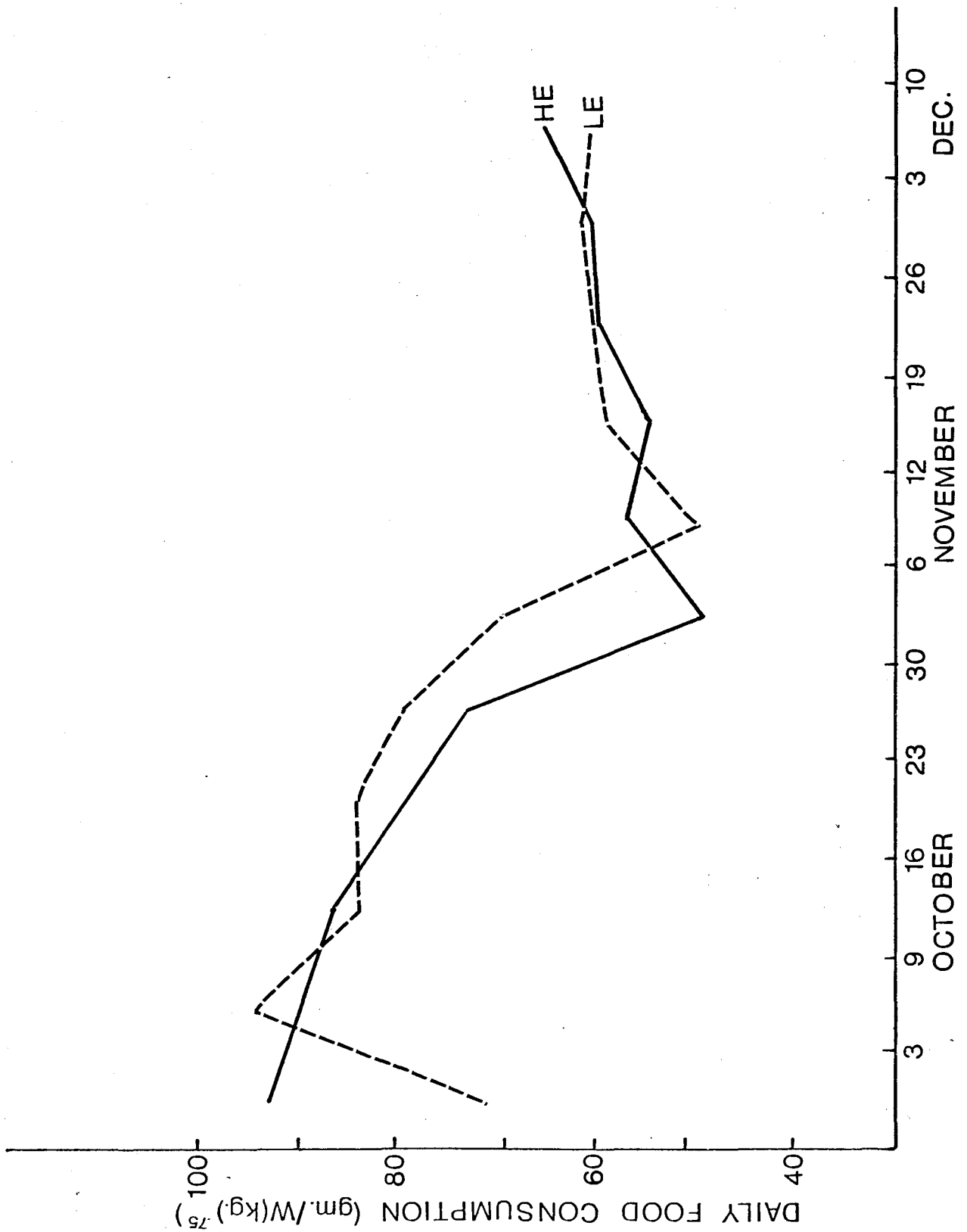
Food Consumption:

The average food consumption (dry matter intake) of the

Table 8. Average Daily Food Consumption and Caloric Intake of H.E. Fawns

| <u>Date</u> | <u>Food Consumption</u> | | <u>Digestible Energy Intake</u> | |
|-------------------|-------------------------|------------------------------------|---------------------------------|------------------------------------|
| | <u>(grams/kg. B.W.)</u> | <u>(grams/W(kg)^{.75})</u> | <u>(kcal./kg. B.W.)</u> | <u>(kcal./W(kg)^{.75})</u> |
| Sept. 29 - Oct. 2 | 40.9 | 93.4 | 131 | 299 |
| Oct. 3 - 9 | 41.6 | 90.7 | 133 | 290 |
| Oct. 10 - 16 | 40.2 | 87.5 | 129 | 280 |
| Oct. 17 - 23 | 36.2 | 80.4 | 116 | 257 |
| Oct. 24 - 30 | 32.0 | 73.3 | 102 | 234 |
| Nov. 1 - 6 | 22.1 | 49.3 | 70.7 | 158 |
| Nov. 6 - 12 | 25.9 | 57.9 | 82.9 | 185 |
| Nov. 13 - 19 | 24.3 | 55.3 | 77.8 | 177 |
| Nov. 20 - 26 | 27.0 | 60.6 | 86 | 194 |
| Nov. 27 - Dec. 3 | 27.0 | 60.9 | 86 | 195 |
| Dec. 4 - 10 | 28.9 | 65.3 | 92 | 209 |

Figure 4. Average daily food consumption ($\text{g/W(kg)}^{.75}$) of the H.E. and L.E. fawns during the fall. L.E. fawns were restricted to ad libitum consumption of H.E. fawns during the previous week.



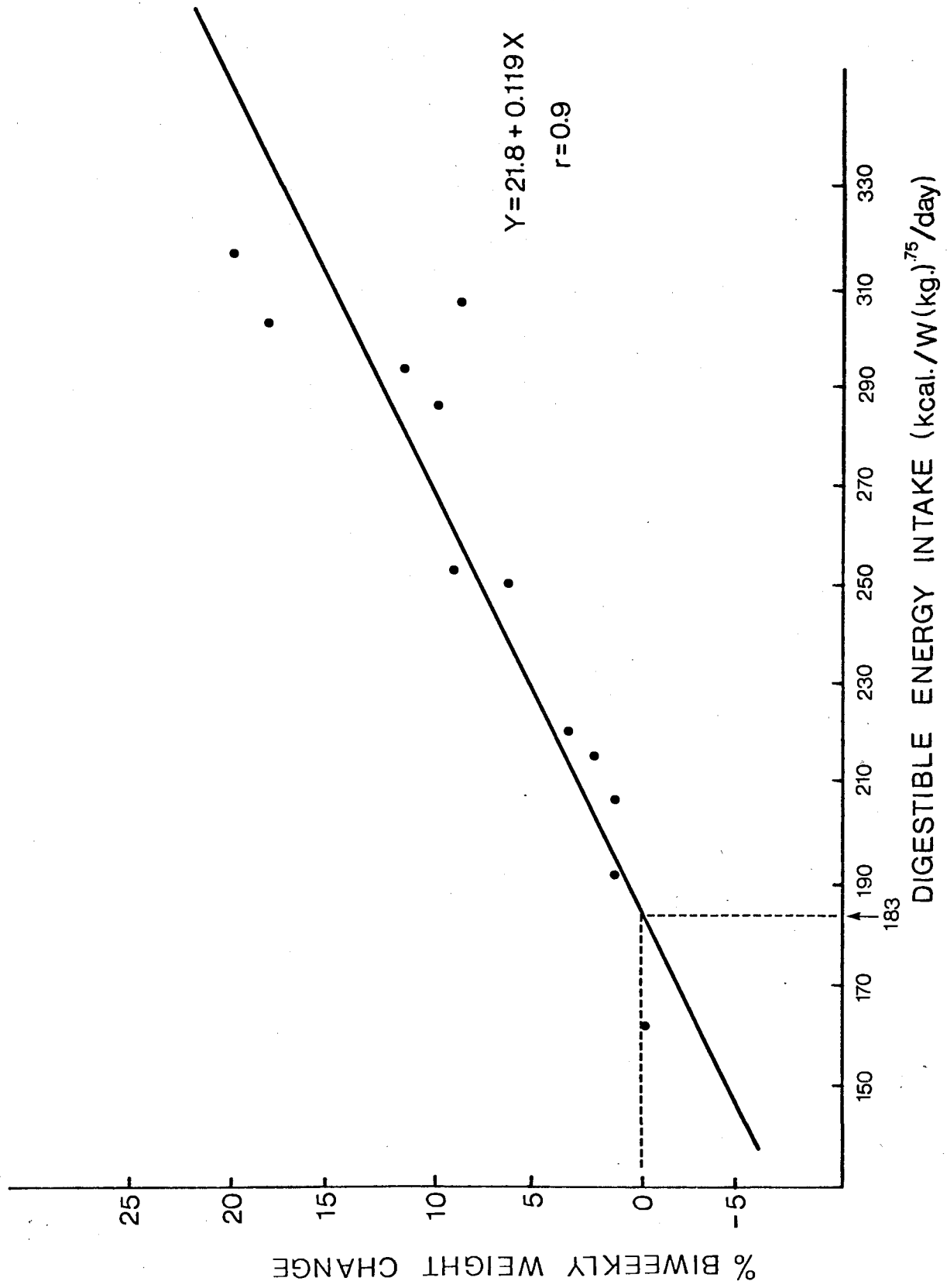
H.E. fawns gradually decreased from 93.4 grams/W(kg)^{.75}/day to 73.3 grams/W(kg)^{.75}/day from the initiation of the experiment until October 31. The following week the consumption dramatically decreased to 49.3 grams/W(kg)^{.75}/day (Table 8, Figure 4). The timing of this decrease in food intake corresponds to the time of the growth halt discussed previously. The food consumption gradually increased subsequently to a level of 65.3 grams/W(kg)^{.75}/day in mid-December. The L.E. fawns were restricted to a similar intake but with a one week time lag (Figure 4).

The gradually decreasing food consumption during the first four weeks of the experiment corresponded to the gradually decreasing growth rate. At this time there is a clear relationship between biweekly digestible energy intake and growth (Figure 5). The digestible energy requirement for zero growth at this time is equal to 183 kcal./W(kg)^{.75}/day. Holter et al. (1977) and Thompson et al. (1973) have found that metabolizable energy (digestible energy - (urinary and methane energy)) in deer is about 88% of digestible energy. Therefore the maintenance metabolizable energy requirement for fawns in the early fall is about 161 kcal./W(kg)^{.75}/day. This is almost identical to the value (162 kcal./W(kg)^{.75}/day) reported for the maintenance requirement of growing white-tailed deer yearlings (Holter et al. 1977) but slightly less than the maintenance requirement of 173 kcal./W(kg)^{.75}/day reported for white-tailed fawns by Thompson et al. (1973).

The average daily food consumption of the H.E. fawns between the start of the experiment and the growth halt in Octo-

35a.

Figure 5. Relationship between digestible energy intake and growth of H.E. fawns prior to the growth halt (Oct. 30).



ber was 85 grams/W(kg)^{.75}/day. This value is almost identical to the daily consumption of 86 grams/W(kg)^{.75}/day reported by Nordan et al. (1970) for black-tailed female fawns of similar size. The average digestible energy intake during this period was 272 kcal./W(kg)^{.75}/day. This value is greater than the daily intake (242 kcal./W(kg)^{.75}/day) of the fawns in the study by Nordan et al. (1970) because the feed in the present experiment had a greater caloric content.

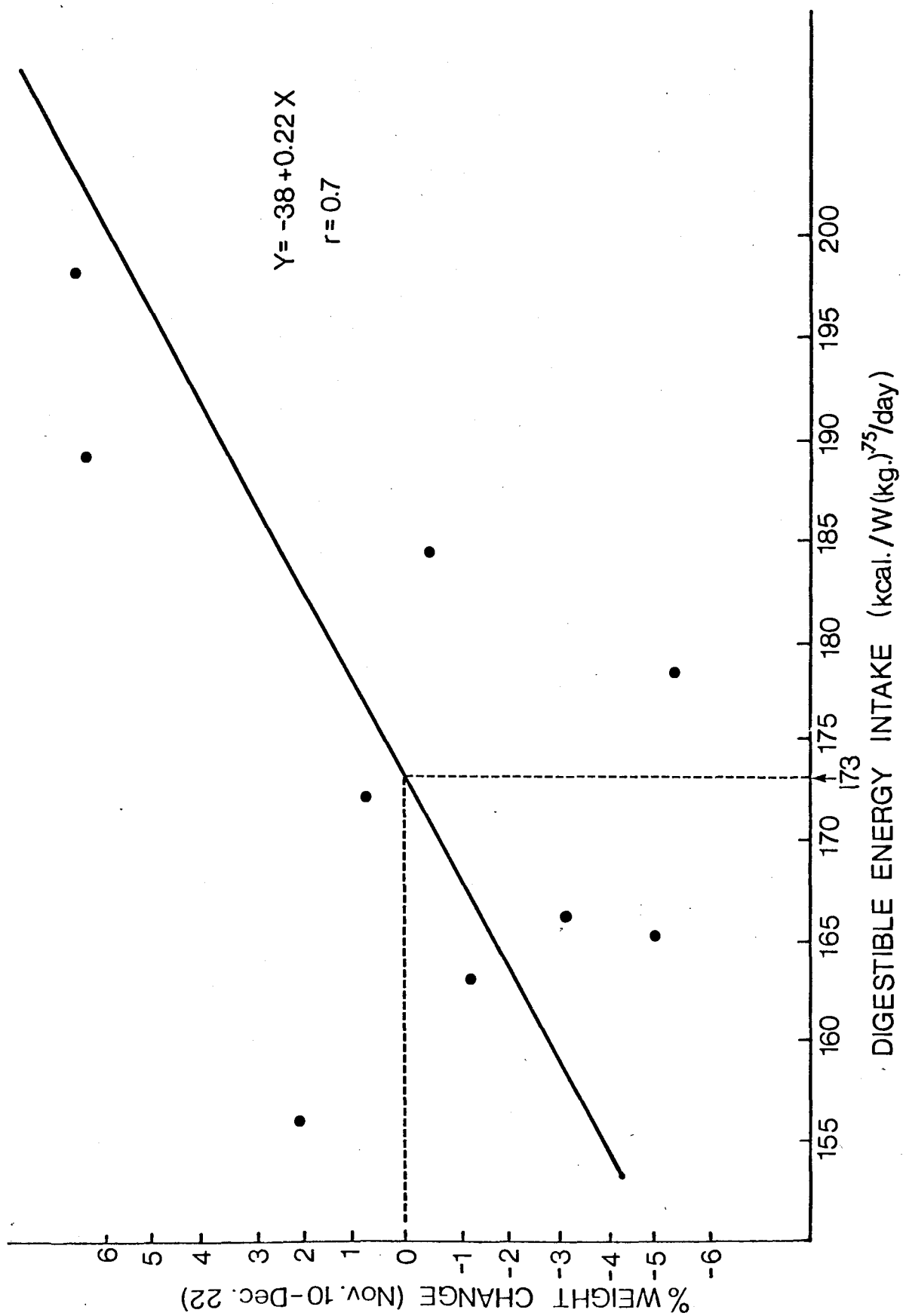
Ammann et al. (1973) demonstrated that deer will eat more to compensate for a lower caloric content in the feed until they are limited by stomach capacity. The fact that the fawns studied by Nordan et al. (1970) did not eat more to increase their energy intake to levels comparable to the present study suggests that they were limited by stomach volume. Therefore it appears that prior to the growth halt in October the fawns eat as much as they can, that is, about 85 grams/W(kg)^{.75}/day. This value is identical to the maximum dry matter intake of white-tailed deer determined by Ammann et al (1973). It is also similar to the daily food consumptions of 95 grams/W(kg)^{.75}/day and 74.2 grams/W(kg)^{.75}/day reported for white-tailed fawns in the early fall (Holter et al. 1976; Thompson et al. 1973). If the food intake of fawns in early fall is limited by the stomach capacity, the energy intake must therefore be dependant on the caloric content of the food.

After the growth halt the food consumption of the H.E. fawns dropped to well below the capacity of the stomach. Between mid-November and late December some fawns in both treat-

ments lost weight and others gained, but overall the weights were essentially stable. Therefore the caloric intake during this period was approximately the maintenance metabolic requirement. The value of this maintenance energy requirement was calculated by regressing the percentage change in body weight from November to December 22 against the average daily digestible energy intake during the same period. This calculation involved both H.E. and L.E. fawns. The average digestible energy requirement to maintain zero growth was $173 \text{ kcal./W(kg)}^{.75}/\text{day}$ (Figure 6). Therefore the maintenance metabolizable energy requirement for fawns in late fall was $152 \text{ kcal./W(kg)}^{.75}/\text{day}$ based on the 88% conversion factor of Holter et al. (1977) and Thompson et al. (1973). This is very close to the daily maintenance requirement of mule deer fawns ($158 \text{ kcal./W(kg)}^{.75}/\text{day}$) and white-tailed deer fawns ($153 \text{ kcal./W(kg)}^{.75}/\text{day}$) in winter (Baker et al. 1979; Holter et al. 1977) but somewhat higher than the value for non-growing white-tailed fawns ($125 \text{ kcal./W(kg)}^{.75}/\text{day}$) reported by Thompson et al. (1973).

The maintenance digestible energy requirement is similar to the estimated values of the digestible energy intake of a wild fawn in Table 5 (153 and $182 \text{ kcal./W(kg)}^{.75}/\text{day}$). Therefore it appears that the maintenance metabolic requirement in the fall is approximately equal to the energy that a wild fawn could obtain from natural browse. The growth halt in October seems to be an adaption which decreases the metabolic requirement to a level which can be satisfied by natural forage at that time of year. The decreased growth and metabolic requirement

Figure 6. Relationship between digestible energy intake and growth of H.E. and L.E. fawns in November and December.



at this time results in a decreased food intake, even when high quality food is provided ad libitum. This voluntary decrease in food intake by captive deer has been reported in previous papers (Holter et al. 1977; Nordan et al. 1968).

Mautz (1978) suggests that deer decrease food intake in winter because in the wild the browse is of such low quality that the energy expenditure of feeding is greater than the energy that can be obtained from the browse. However it seems more likely that the decrease in feeding by captive deer is due to a reduction of the metabolic demands to a level that can be supported by natural browse at that time of the year. Wild deer would be expected to eat as much as they can. However, deer in the wild and captive deer which are fed only browse also decrease their winter food intake (Alldredge et al. 1974; Ozoga and Verme 1970). This is probably due to the decreased digestibility of winter browse which would slow the passage of the food through the digestive tract. Ammann et al. (1973) found that as the digestibility of food decreases below 50% the dry matter intake also decreases due to a decreased rate of passage. Since the digestibility of browse decreases below 50% in winter this is probably the cause of the observed decreased food intake in the wild. I suspect that as long as food is available in the wild a deer will eat as much as it can.

Protein Intake of Experimental Animals:

The crude protein content of the L.E. feed was 21% and of the H.E. feed was 19.6%. These values are slightly below the 25.2% and 22% protein concentrations reported for maximum growth of white-tailed fawns (Smith et al. 1975; Ullrey et al. 1967).

However the protein content of the feeds was about twice that found in natural browse (Table 4). The average daily intake of crude protein over the duration of the experiment was 13.4 grams/ $W(\text{kg})^{.75}$ /day for the H.E. fawns and 14.9 grams/ $W(\text{kg})^{.75}$ /day for the L.E. fawns. Since the protein intake of the treatments was very similar any effect due to the small differences seems unlikely. In fact, any observed detrimental effect of the L.E. treatment cannot be due to insufficient protein because the L.E. fawns received more protein than the H.E. fawns.

Reliability of Progesterone Assays:

There are several possible sources of error in the progesterone data. Weekly sampling may have been insufficient to detect changes that were occurring on a daily or circadian level. The progesterone antibody used in the assays was not specific for deer progesterone and therefore may not have been binding completely effectively. There may have been some cross-reactivity with other steroids although the antibody used was quite specific. Stress to the animals during sampling can cause the release of adrenal progesterone in deer (Wesson et al. 1979). This was a potential problem in the present study. However, since the sampling regime was always the same, any stress effect would likely remain constant. Although absolute values may be altered by stress, relative changes should represent real changes in ovarian progesterone levels. The problem of stress is further dealt with in the discussion.

Plasma Progesterone Levels Prior to Breeding Season:

The breeding season of wild black-tailed deer on Vancouver

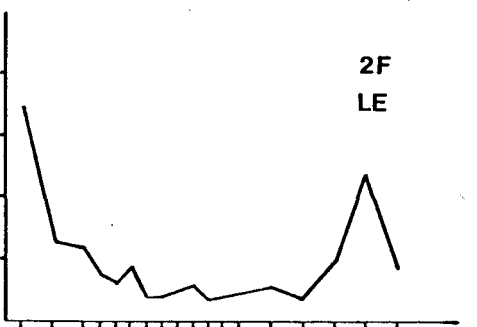
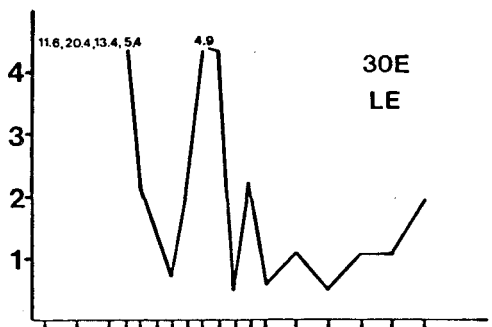
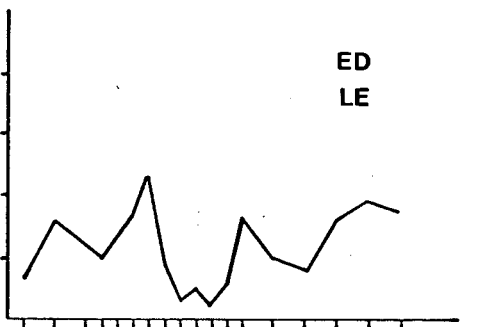
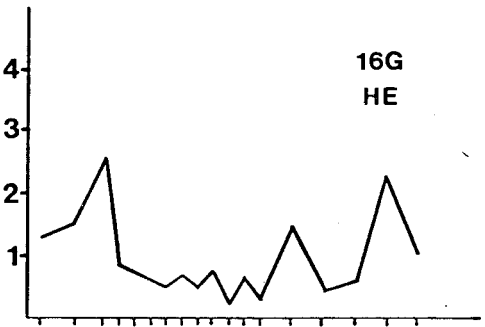
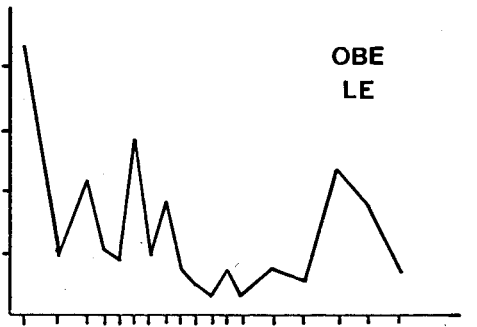
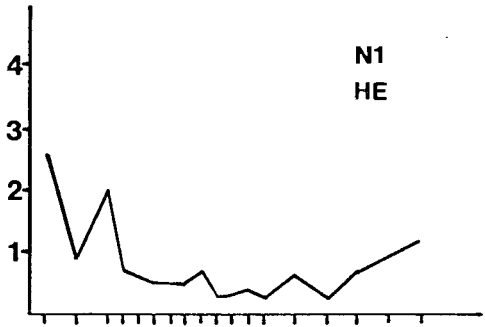
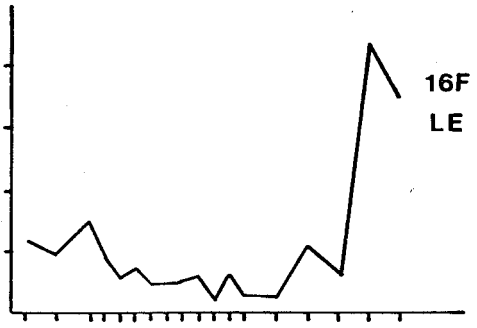
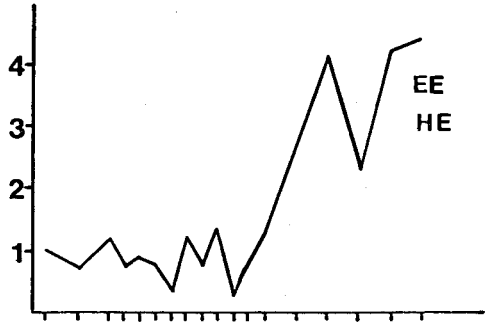
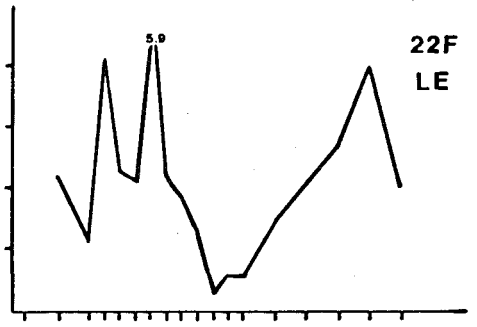
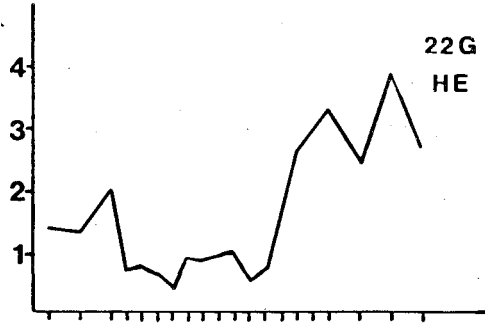
Island begins about November 4 (Thomas 1970). Similarly, the breeding season of the captive herd began early in November in previous years (Mueller 1977). Plasma progesterone levels of the experimental fawns prior to the breeding season, between September 26 and October 24, averaged 2.9 ± 4.3 ng./ml. (n=29). Values ranged from 0.7 to 4.3 ng./ml. in all animals except #30E which had extremely high progesterone values ranging from 11.6 to 20.4 ng./ml. (Figure 7). These values are higher than would be expected for anestrus adult females. Plasma progesterone levels less than 0.5 ng./ml. have been found in anestrus, adult, white-tailed and roe deer females (Plotka et al. 1977; Hoffmann et al. 1978). Anestrus sheep and cattle have similar low progesterone levels (Yuthasastrakosol et al. 1975; Donaldson et al. 1970).

Nalbandov (1976) and Ramaley (1979) reported that prepubertal, female mammals undergo a series of non-ovulatory cycles prior to first ovulation. Thomas and Cowan (1975) found that non-ovulatory cycles also occur in adult black-tailed does prior to the breeding season. Elevated progesterone levels accompany such cycles in rats (Meijs-Roelofs et al. 1975) and fluctuations in plasma progesterone indicative of several ovarian cycles can occur in prepubertal heifers prior to first estrus (Donaldson et al. 1970). Similar but less extreme increases in progesterone have been reported in pre-pubertal heifers (Gonzalez-Padilla et al. 1975; Shotton et al. 1978) and lambs (Fitzgerald and Butler 1978; Ryan and Foster 1978). However increased levels of progesterone were not detected in the pre-pubertal white-tailed

42a.

Figure 7. Plasma progesterone levels of fawns during the fall

PLASMA PROGESTERONE (ng./ml.)



26 10 24 10 24 8 22 5 20 3 17 17 12
Oct. Nov. Dec. Jan. Feb. M. Apr.

26 10 24 10 24 8 22 5 20 3 17 17 12
Oct. Nov. Dec. Jan. Feb. M. Apr.

Breeding Season

Breeding Season

deer fawns studied by Abler et al. (1976).

The source of the pre-pubertal progesterone in rats is primarily ovarian (Meijs-Roelofs et al. 1975) and probably comes from luteinized follicles because there are no corpora lutea present at this time in cows or lambs (Donaldson et al. 1970; Ryand and Foster 1978). The ovaries of the fawn (N2) that died accidentally early in November contained a large number of follicles with greatly thickened theca interna (Figure 8). Possibly the elevated progesterone levels of the fawns prior to the breeding season resulted from lutenized thecal cells in preovulatory follicles.

Behavioral Indicators of First Estrus:

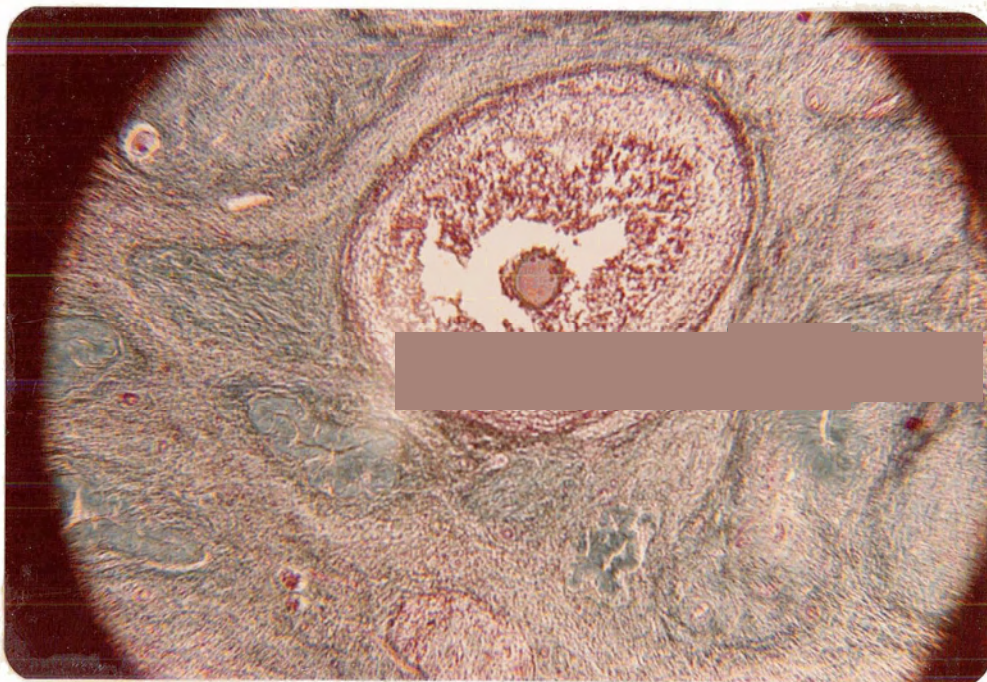
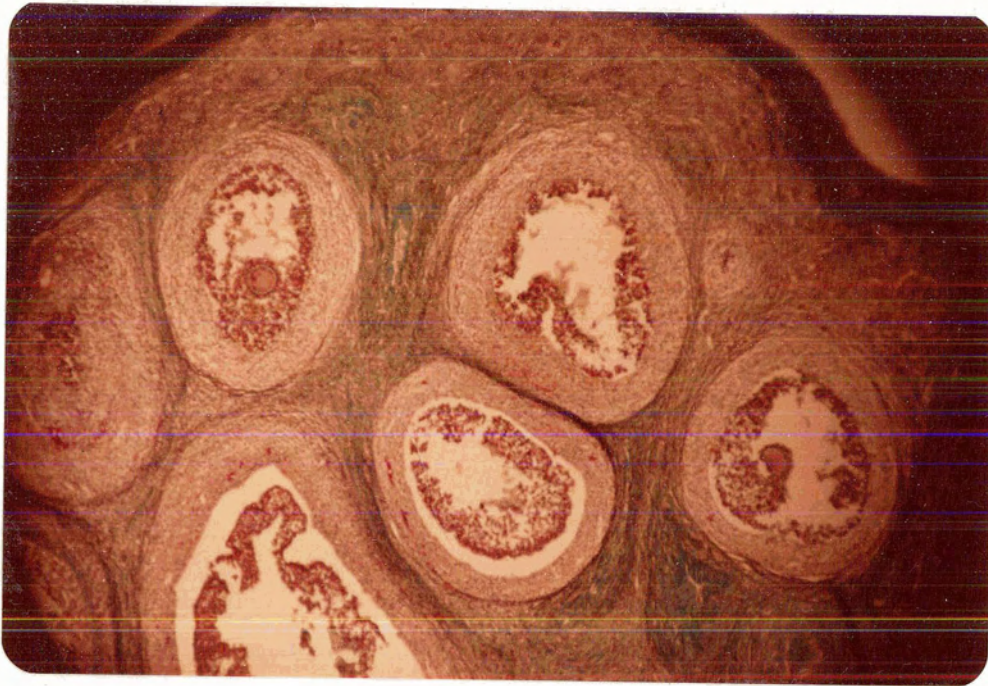
None of the fawns were observed to copulate during November and early December when they were placed with a buck for 4 hours daily and observed. Similarly, the pedometers recorded no sudden increases in daily activity indicative of estrus behavior (West 1968). However the activity data was fragmentary because the pedometers were frequently broken. The fawns never exhibited receptive lordosis behavior when they were pressed on the rump which suggests that they were not in estrus. However, testing for lordosis behavior is reliable only for very tame deer (West 1968) and since the deer in this experiment were not very tame the results may not be dependable. Therefore, puberty attainment was judged on the basis of plasma progesterone levels and conception.

Plasma Progesterone Levels During the Breeding Season:

During the breeding season (early November to January 5)

44a.

Figure 8. Photomicrographs of follicles in ovary of fawn N2, early November. Enlarged theca is indicated.



there appeared to be 2 different patterns of plasma progesterone levels. Five fawns (22G, 16G, 2F, N1, 16F) had constantly low levels averaging 0.58 ng./ml. and ranging from 0.17 to 1.00 ng./ml (Figure 7). The other 5 fawns had fluctuating levels of progesterone which averaged 1.30 ng./ml. and ranged from 0.23 to 5.94 ng./ml. These high, fluctuating values suggest ovarian cycling. The observed upper values are comparable to cycling levels of progesterone found in adult white-tailed deer (Plotka et al. 1977), roe deer (Hoffmann et al. 1978), sheep (Yuthasastrakosol et al. 1975) and cows (Donaldson et al. 1970). The ovarian activity could have been: i) normal estrus cycles, ii) ovulations with silent heats, or iii) non-ovulatory cycles.

It is tempting to suggest that the other 5 fawns with constant, low, progesterone levels represent non-cycling fawns. However one of these fawns (#22G) became pregnant and therefore must have cycled. This individual had slightly higher progesterone levels than the other 4 in this group but the difference was not distinct. Therefore, although the progesterone values of the other 4 fawns suggest that they did not cycle, the weekly blood sampling may have been insufficient and high levels could have been missed.

The progesterone levels of individuals during the breeding season showed no pattern in relation to the levels prior to the breeding season. All fawns had plasma progesterone levels suggesting ovarian activity in September and October but the graphs indicate that early in November progesterone levels decreased in 5 of the animals. This apparent decrease in ovarian activity

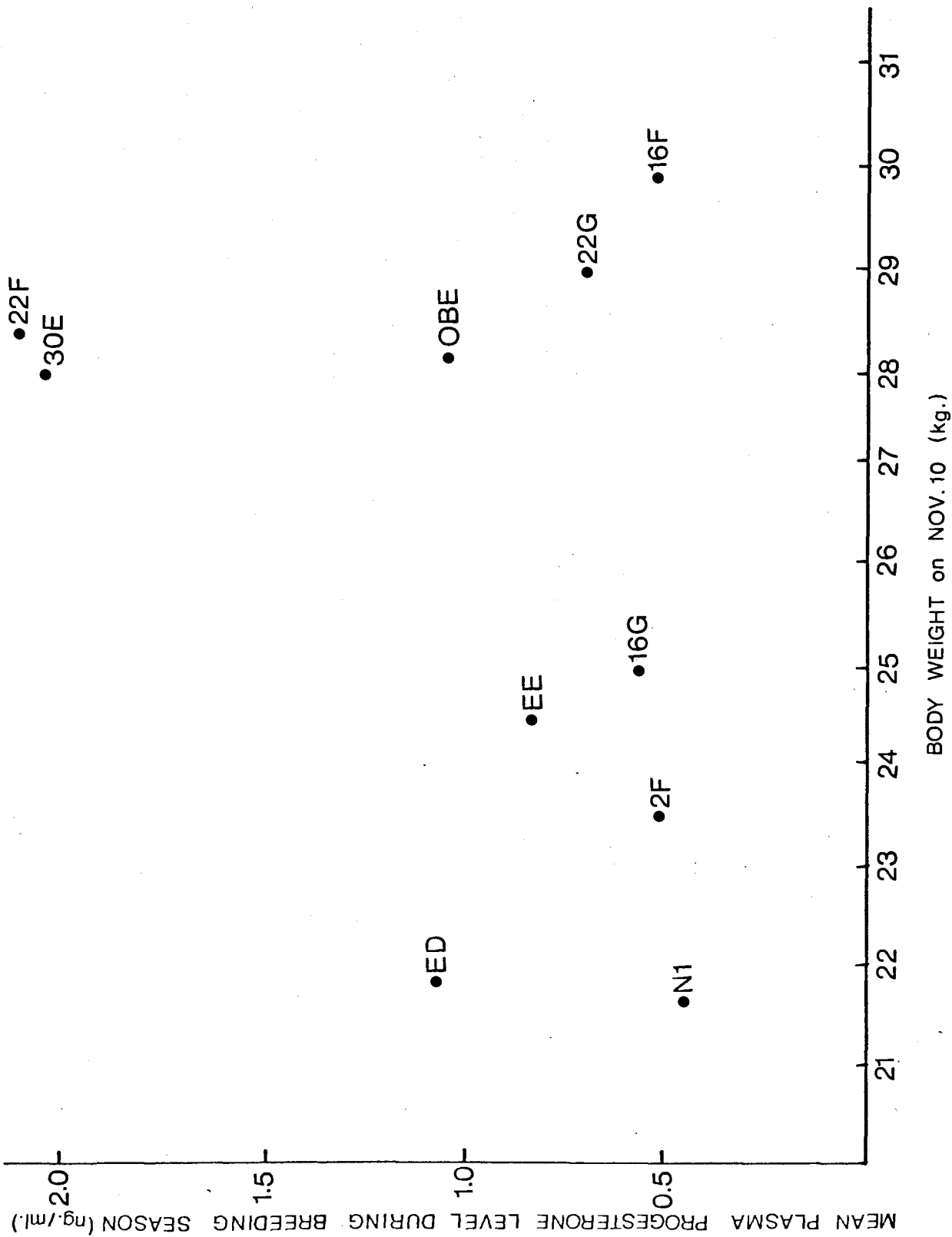
corresponded in time with: i) the initiation of the normal adult breeding season, ii) the growth halt in the fawns, and iii) the daily introduction of the fawns to the breeding buck. Possibly all prepubertal fawns experience ovarian cycles, which may or may not be ovulatory, but ovarian activity is inhibited by the onset of the breeding season or the presence of a buck if the individual is not physiologically otherwise prepared to breed. Similarly, several of the fawns (#ED, 22F, OBE) that had high progesterone values in November exhibited reduced levels during the period that they were kept with the buck constantly in December and January.

Relationship Between Body Weight and Ovarian Activity During the Breeding Season:

The body weight of each fawn on November 10 was used to determine if body weight during the breeding season had any relationship to progesterone levels as an indicator of ovarian activity. The growth halt had occurred prior to this date and subsequently individual fawns did not change in body weight to any significant degree. The smallest fawn weighed 28% less than the heaviest so there was a substantial range of body weights. There was no significant difference ($p > 0.05$) between the body weight of cycling fawns (26.7 ± 2.9 kg.) and the mean body weight of the 4 fawns that apparently did not cycle (24.9 ± 3.52 kg.). Similarly, there was no correlation between body weight and the average plasma progesterone level during the breeding season (Figure 9). This result is contrary to other studies which have found that the commencement of ovarian cycles

47a.

Figure 9. Mean progesterone level of fawns during the breeding season compared with their body weight on November 10.



is related to body weight (eg. rats: Kennedy and Mitra 1963; lambs: Foster and Ryan 1978). The small sample size and the uncertainty regarding whether or not the animals with low progesterone values cycled makes the present results inconclusive. However several fawns certainly had progesterone levels indicative of ovarian cycling at body weights comparable to wild fawns (16 - 30 kg.; Mueller 1977). Yet Thomas (1970) found that although wild fawns commonly develop large and ruptured follicles during the breeding season, corpora lutea rarely develop. He found only one example of a corpora lutea developing in a wild fawn in a sample of 70 pairs of ovaries. Therefore, although many wild fawns attain a body weight that is comparable to captive fawns with high progesterone levels, they do not exhibit normal estrus cycles.

Relationship Between Caloric Intake and Ovarian Activity During the Breeding Season:

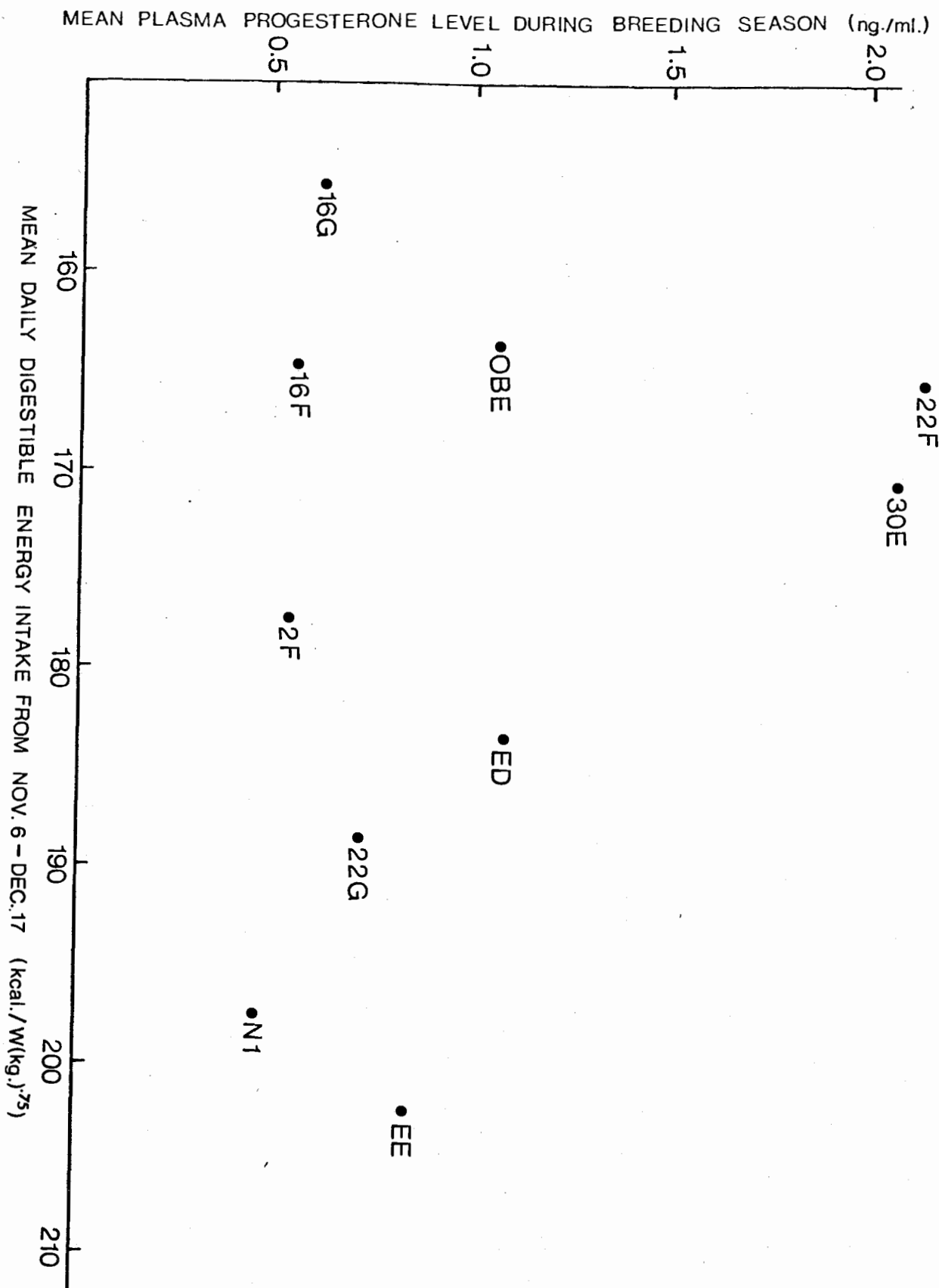
There was no significant difference ($p > 0.05$) between the mean daily caloric intake of the 6 cycling fawns during the breeding season ($180 \pm 15.1 \text{ kcal./W(kg)}^{.75}$) and that of the 4 fawns that apparently did not cycle ($174 \pm 18.2 \text{ kcal./W(kg)}^{.75}$). The average daily intake between November 6 and December 17 was used to represent caloric intake during the breeding season. Similarly, there was no significant difference ($p > 0.05$) in the average daily caloric intake of the cycling and non-cycling fawns over the entire fall from September 26 to December 17 (212 ± 13.6 vs. $208 \pm 21.3 \text{ kcal/W(kg)}^{.75}$). There was no correlation between average daily caloric intake and average pro-

gesterone value during the breeding season (Figure 10). The interaction of body weight and caloric intake also had no significant effect on the average progesterone value during the breeding season.

These results differ from those of a similar experiment on white-tailed fawns by Abler et al. (1976). However these workers only bled their fawns once a month and therefore could have missed progesterone peaks. They did not measure the food consumption of individual fawns and did not restrict the food consumption of the L.E. fawns and therefore the L.E. fawns compensated by eating more. They claimed that there was still a difference in caloric intake between groups of fawns in their study but the caloric content of the feeds was based on data for sheep. White-tailed fawns may have been more efficient than sheep at digesting the low energy diet, as were the fawns in the present experiment. This is supported by the fact that the L.E. diet had no effect on the growth rate of the fawns (Kirkpatrick et al. 1975). Therefore it is likely that there was actually no difference between the energy intakes of the H.E. and L.E. treatments so that the results may be entirely spurious.

In domestic animals, very high and very low caloric intakes are detrimental to reproduction compared to an intermediate level (Sadleir 1969). Lamond et al. (1973) reported that high energy diets decrease fertility by reducing the ovulation rate and low energy diets result in a reduced fertilization rate in adult ewes. However, Memon et al. (1969) found that high energy diets increased the ovulation rate in ewes.

Figure 10. Mean progesterone level of fawns during the breeding season compared with their mean daily intake of digestible energy from November 6 to December 17.



The results of the present experiment are inconclusive because I cannot be certain that individuals with low progesterone values did not cycle. However it is clear that several fawns had progesterone levels indicative of cycling on caloric intakes comparable to that calculated for wild fawns. Thus wild fawns attain a body size and obtain a caloric intake similar to captive fawns which have high progesterone levels but wild fawns do not exhibit normal ovarian cycles. This suggests that either some other factor prevents cycling in wild fawns or that the elevated progesterone levels in the experimental fawns do not necessarily indicate normal cycles.

Conception by the Fawns:

Although 6 fawns apparently cycled, only 1 of these (22G) conceived and subsequently gave birth. Pregnancy was detected by the presence of a fetal skeleton in a X-ray taken on April 12. This female gave birth to a healthy, 2 kg, female fawn on July 18 which can be back-dated by 203 days to give a conception date of about December 23 (Golley 1957).

In a previous study of puberty attainment on this herd of black-tailed deer 45% to 71% of female fawns conceived and gave birth in 3 consecutive years (Mueller 1977). Mueller found that precocious fawns were significantly heavier than non-precocious fawns and that the lightest fawn which conceived weighed 24 kg. at 175 days of age. In the present experiment 3 fawns weighed less than 24 kg. at 175 days of age and thus were probably too small to conceive even though one of them (ED) had high progesterone levels. Of the remaining 7 fawns that were

large enough, 3 were on the H.E. diet and 4 received the L.E. diet. However due to a voluntary low food intake one of the H.E. fawns (16G) had a daily caloric intake comparable to the L.E. fawns. Therefore, of the 7 fawns of suitable size to breed, 2 had relatively high mean daily caloric intakes and 5 had reduced caloric intakes (Table 9). One of the high caloric intake fawns conceived and 0 of 5 low caloric intake fawns conceived. The conception rate of the high caloric intake fawns is comparable to the rate found by Mueller (1977) in a large sample of fawns raised on high energy diets fed ad libitum. The 0 of 5 conception rate in the reduced caloric intake fawns is significantly less ($p = 0.02$) than the 50% rate reported by Mueller. 2 of the low caloric intake fawns apparently did not cycle and 3 cycled but did not conceive. Therefore, although the energy reduction did not appear to affect the incidence of ovarian cycling it did appear to prevent conception from occurring. Similarly, low energy diets decrease the fertilization rate in adult, domestic ewes (Lamond et al. 1973).

The failure to conceive in females that were apparently cycling may have been caused by silent heats, that is, ovulations without estrus. None of the fawns were observed to copulate or exhibit estrus behavior even though some had high progesterone levels. Adult female black-tailed deer almost always have a silent heat prior to breeding (Thomas 1970). In pubertal heifers, silent heats accompany up to 74% of first ovulations, 43% of second ovulations and 21% of third ovulations (Morrow 1969). Underfed rats also often fail to exhibit estrus during

Table 9. Mean Daily Caloric Intakes of Fawns During Breeding Season

| <u>High Caloric Intake Group</u> | | <u>Low Caloric Intake Group</u> | |
|----------------------------------|-------------------------------|---------------------------------|-------------------------------|
| EE | 204 kcal/W(kg) ^{.75} | 30E | 172 kcal/W(kg) ^{.75} |
| 22G | 189 " | 22F | 166 " |
| \bar{X} | 196 " | 16F | 165 " |
| | | OBE | 164 " |
| | | 16G | 156 " |
| | | \bar{X} | 165 " |

- high caloric intake group had a significantly greater intake than low caloric intake group $p < 0.02$, $F_{(1,5)} = 30.8$.

Fawns Less Than 24kg. at 175 days of age

N1 22.2 kg.
2F 22.1 kg.
ED 21.7 kg.

their first several ovulations (Kennedy and Mitra 1962). Therefore, reduced caloric intake may inhibit estrus and thereby prevent conceptions.

Progesterone Levels After the Breeding Season:

Between January 20 and April 12 the pregnant female (22G) had an average plasma progesterone levels of 2.8 ng./ml. (range 2.4 - 3.8). This level is slightly lower than the average progesterone levels of pregnant, adult, white-tailed deer (4.6 ng./ml.; Plotka et al. 1977) and roe deer (4.0 ng./ml.; Hoffmann et al. 1978).

Non-pregnant fawns that had cycled during the breeding season continued to have relatively high progesterone levels from January to April (\bar{X} = 2.1, range 0.53 - 5.9 ng./ml.). In addition, the 4 fawns that did not appear to cycle during the breeding season had high levels after the breeding season (\bar{X} = 1.3, range 0.3 - 5.7 ng./ml.). These high levels occurred primarily at the mid-March sampling date when all non-pregnant animals had high progesterone values (\bar{X} = 2.9, range 1.1 - 5.7 ng./ml.). Presumably ovulatory cycles continue to occur long after the breeding season if the deer does not become pregnant. Similarly, Plotka et al. (1977) detected cycling levels of progesterone in 2 non-pregnant white-tailed does in early March. Therefore, it is not possible to diagnose pregnancy in black-tailed or white-tailed deer on the basis of progesterone levels, at least prior to mid-March.

General Discussion

The hypotheses that were tested in this study were:

- 1) Puberty in female black-tailed deer fawns is dependant upon a sufficient caloric intake during the fall.
- 2) Wild fawns are unable to obtain this necessary level of caloric intake from natural browse and thus do not breed.

If puberty is defined as the period in life when successful reproduction is first possible, then this experiment provides evidence which supports the 2 hypotheses. The maintenance digestible energy requirement for the fawns during the fall was about $173 \text{ kcal/W(kg)}^{.75}/\text{day}$. The 5 fawns with a daily caloric intake close to this maintenance level ($156 - 172 \text{ kcal/W(kg)}^{.75}$) all failed to conceive. The only fawn which successfully bred was 1 of 2 which had a much higher caloric intake. Similarly, about 50% of female fawns receiving a high energy intake during previous years successfully conceived (Mueller 1977). This suggests that the caloric intake of female fawns during the fall must be in excess of the maintenance requirement in order for them to breed. Presumably this allows them to deposit fat for use later in the winter during gestation.

The calculated intake of a wild fawn ($153 - 182 \text{ kcal/W(kg)}^{.75}/\text{day}$) is close to the maintenance level. Therefore it appears that the caloric intake of a wild fawn is insufficient for successful reproduction to occur.

The way in which puberty is inhibited by low energy intake is not clear. The use of progesterone levels to interpret

ovarian activity in this experiment was inconclusive. In most female mammals, elevated progesterone levels would indicate that ovulation has occurred and a corpus luteum is functioning. However in this experiment, fawns had high progesterone levels before and after the breeding season which presumably came from stimulated follicles or interstitial cells. Therefore, high progesterone levels during the breeding season may not be indicative of normal ovarian cycles in this experiment. Due to the uncertainty of the relationship between progesterone levels and ovarian activity there are 2 possible explanations for the observed results:

- 1) The high progesterone levels of some of the fawns during the breeding season may have come from follicles, not corpora lutea. Since wild fawns often develop large follicles they may also have elevated progesterone levels during the breeding season. If so, one would not expect that body weight or restriction of energy intake to levels comparable to the wild would have any effect on progesterone levels.
- 2) The high progesterone may represent normal ovulation and corpora lutea formation. If so, the experimental fawns were quite different from wild fawns which almost never form corpora lutea (Thomas 1970). Since the fawns in the experiment had high progesterone levels at weights and caloric intakes comparable to wild fawns, some other factor would be needed to explain the difference between captive and wild fawns. The most obvious nutritional difference would be the protein intake. However, studies of deer and domestic animals suggest that protein is un-

important in influencing productivity and ovarian activity (Abler et al. 1976; Lamond et al. 1973; Memon et al. 1969).

The best way to determine which explanation is most likely correct would be to measure progesterone levels of some wild fawns during the breeding season. If they were secreting progesterone but had no corpora lutea, it would indicate that progesterone levels in the experimental fawns do not necessarily mean the animal has ovulated. However, there is no data available on progesterone levels in wild fawns. The only clue available is a few ovarian sections from 2 captive fawns, in addition to N2, from the S.F.U. herd that died during previous breeding season. These sections contain developing follicles but no corpora lutea. It seems likely that they would have had high progesterone levels because they were raised under similar conditions to the fawns in present experiment. Therefore there is reason to believe that elevated progesterone levels in female black-tailed deer fawns during the breeding season often do not result from ovulation and corpora lutea formation. If so, some other technique such as laproscopy would be necessary to determine the ovarian activity of the fawns. Overall, the interpretation of the elevated progesterone values is uncertain but it seems likely that they do not necessarily indicate normal ovarian cycling.

The caloric intake of a wild fawn is probably insufficient for successful reproduction to occur but the way in which puberty is inhibited is not clear. Reduced caloric intake may:

- i) inhibit ovulation

- ii) inhibit estrus
- iii) inhibit implantation
- iv) cause early resorption

Black-tailed deer fawns in the wild almost never breed and it is unlikely that any feasible management technique could change this. However it should be possible to increase the productivity of yearlings and white-tailed fawns by increasing the availability of browse species with high digestible energy.

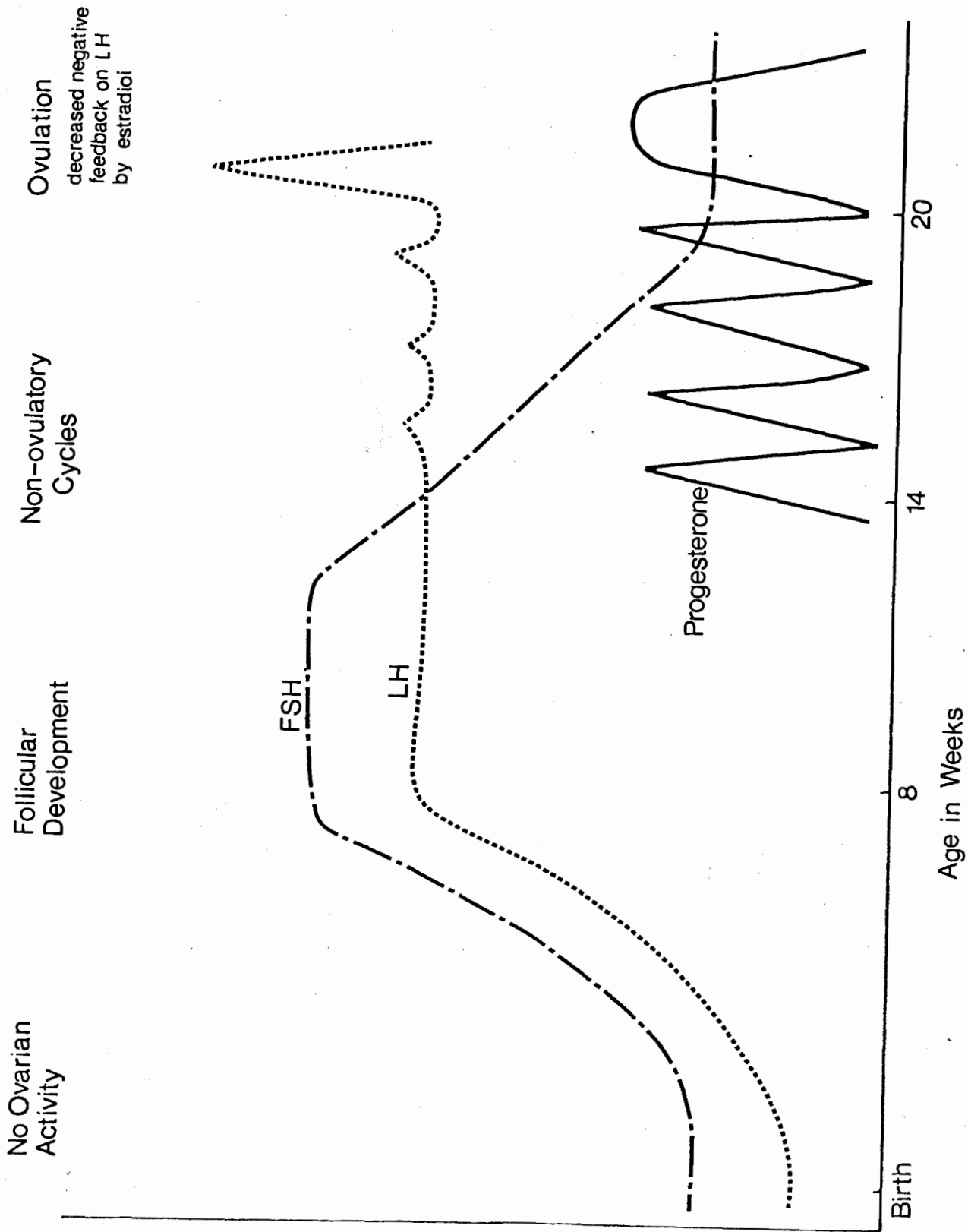
General Model of Puberty Attainment (Figure 11)

Newborn female mammals initially secrete low levels of L.H. and F.S.H. but levels of both gonadotropins increase early in life. This increase occurs at about 1 week of age in rats (Ramaley 1979) and at about 8 weeks of age in lambs (Foster et al. 1975; Fitzgerald and Butler 1978). Gonadotropin stimulation results in pre-pubertal, non-ovulatory ovarian cycles about the time of weaning in rats and lambs (Ramaley 1979). This period is marked by increased plasma progesterone levels, which are apparently caused by luteinization of pre-ovulatory follicles. This may explain the elevated progesterone levels of the prepubertal fawns in the present experiment. The increased progesterone level may cause the decrease in F.S.H. that occurs at this time in rats (Meijs-Roelofs et al. 1975) and lambs (Fitzgerald and Butler 1978; Foster et al. 1975). Gonzalez-Padillo et al. (1975) and Ryan and Foster (1978) propose that the progesterone may be important in initiating and synchronizing the L.H. surges of the estrus cycle.

The first ovulatory surge of L.H. in lambs does not occur

59a.

Figure 11. General pattern of events during puberty in mammals. See text for explanation.



No Ovarian Activity

Follicular Development

Non-ovulatory Cycles

Ovulation
decreased negative feedback on LH by estradiol

FSH

LH

Progesterone

Birth

8

14

20

Age in Weeks

until there is a decrease in the responsiveness of the hypothalamus to the negative feedback of estradiol on tonic L.H. levels (Foster and Ryan 1978). Prior to this decrease in responsiveness, the basal levels of estradiol inhibit tonic L.H. levels and thus prevent the ovulatory L.H. surge. The decrease in responsiveness is related to body weight in lambs (Foster and Ryan 1978) and to photoperiod in adult sheep (Legan and Karsch 1979). This may be the mechanism that results in most female mammals not breeding until a critical weight is attained (see Introduction). In the present experiment there was no evidence that ovarian activity was influenced by body weight. However the value of progesterone levels to interpret ovarian activity was questionable. Certainly the results of Mueller (1977) indicate that puberty attainment in black-tailed fawns is influenced by body weight.

After an individual critical weight has been reached, other factors can still influence the onset of puberty. In female mice a male pheromone accelerates the onset of puberty after the critical weight is reached (Vandenbergh et al. 1972). Stress in the form of temperature extremes, noise, handling etc. has been shown to accelerate puberty in some cases and delay puberty in others (Ramirez 1973, Ramaley 1974). Therefore stress to the animals must be considered when experiments on puberty are undertaken. This is the reason that blood sampling was only done once a week.

It is possible that some of the variation in progesterone levels was due to stress. Wesson et al. (1979) demonstrated

that the stress of blood sampling, especially when succinyl choline is used for immobilization, can cause an increase in progesterone levels. They suggest that this progesterone is from the adrenals. However, my sampling routine was always the same so that although it may have resulted in a change in the absolute amount of progesterone, this change would probably be relatively constant. The major changes in the relative amounts of progesterone suggest that other factors are involved. Major increases occurred in most animals after the breeding season at a time when the stress to the animals was probably the least. Also, Wesson et al. (1979) reported that stress induced progesterone increases did not occur if tranquilizing drugs were used. The final 2 samples in the present experiment were done using Xylazine and the fawns were subconscious during the blood sampling. However progesterone levels were still high in most of the fawns. Therefore, although some of the variation in progesterone levels may be due to stress, the overall pattern probably represents real changes in ovarian secretion.

There was some indication that the presence of the buck may have inhibited ovarian activity in the present experiment. All fawns had high progesterone levels in October but when daily 4 hour introductions to the buck began, 5 animals exhibited a drop in progesterone for that period. In mid-December when the fawns were placed with the buck continually, 3 more fawns exhibited lower progesterone levels. After mid-January when the buck was removed, progesterone levels increased again

in all fawns. Therefore the buck may have caused stress and thereby depressed ovarian progesterone secretion. Alternatively, ovarian activity may be inhibited by a buck if the female is not physiologically prepared to breed.

The level of nutrition subsequent to reaching the critical body weight can effect puberty attainment. Underfed rats begin follicular development when they attain the critical body weight but do not ovulate until adequate food is provided (Kennedy and Mitra 1963; Lintern-Moore and Everitt 1978). Underfed rats also often fail to exhibit estrus during their first few cycles. The level of caloric intake in the present experiment did not appear to influence ovarian activity as represented by progesterone values. However, low energy intake did seem to reduce the conception rate.

It seems likely that body size and caloric intake may interact to regulate puberty. As body size increases the volume of the rumen and potential food intake increases at a greater rate than the metabolic requirement. Therefore larger animals can more easily obtain their metabolic requirement of energy. This would explain why yearling females and white-tailed fawns are able to attain puberty feeding on the same foods as black-tailed fawns. Since they are larger they would have a greater rate of caloric intake relative to their requirements. Therefore they would be more likely to have an excess of caloric energy to devote to reproduction.

Pattern of Growth and Energetics

The deer fawns displayed a rapid growth rate throughout

the summer (0.18 kg/day) which continued into October. They appear to be eating as much as they can at this time and are probably growing at their maximum rate. The digestible energy intake in the early fall was $295 \text{ kcal/W(kg)}^{.75}/\text{day}$. Growth rate and food consumption began to decrease in mid-October and at the end of October an abrupt growth halt and decline in food intake occurred. The maintenance digestible energy requirement after the growth halt ($173 \text{ kcal/W(kg)}^{.75}/\text{day}$) was within the range of intakes calculated for wild fawns at this time (153 - $183 \text{ kcal/W(kg)}^{.75}/\text{day}$). Therefore the growth halt appears to be an adaptation which reduces the metabolic demand to a level that can be supported in the wild. This suggests that the pattern of growth and fat deposition in deer is genetically programmed and that the pattern in captivity will be essentially the same as the pattern in the wild.

Conclusions

1. Restriction of caloric intake appeared to prevent successful reproduction in 5 female black-tailed deer fawns even though they had attained body weights comparable to fawns which did breed.
2. A wild fawn would be unable to obtain a sufficient level of caloric intake from natural browse to allow successful breeding.
3. Fawns exhibit elevated progesterone levels before, during and after the breeding season. The source of at least some of this progesterone may be enlarged ovarian follicles. Therefore elevated progesterone levels do not necessarily indicate normal ovarian cycles.
4. The presence of a buck appeared to inhibit progesterone secretion by female fawns.
5. Fawns grow rapidly until mid-October but growth virtually halts by the end of October. This growth halt reduces the caloric requirement of fawns to a level which a wild fawn could obtain from browse at that time of the year.

Appendix I. Variation in Progesterone Radioimmunoassays

Since 2 different radioimmunoassay kits (Biokit and New England Nuclear) and 2 different extraction solvents (diethyl ether and petroleum ether) were used to do the assays, 22 samples were reassayed in order to determine if the different assay techniques were comparable. These samples had originally been extracted with diethyl ether and 9 had been assayed with the Biokit and 13 had been assayed with the NEN kit. The replicate assay was done with petroleum ether and the NEN kit.

| Sample | Original Technique | Original Progesterone Value (ng/ml) | Replicate Progesterone Value (ng/ml) |
|--------------|--------------------|-------------------------------------|--------------------------------------|
| Dec. 22, 30E | BIO & DE | 0.3 | 0.5 |
| Nov. 24, 16F | " | 0.5 | 0.5 |
| Dec. 15, ED | " | 0.6 | 0.6 |
| Dec. 15, OBE | " | 0.5 | 0.7 |
| Dec. 1, 22F | " | 2.2 | 1.9 |
| Dec. 22, 16F | " | 0.2 | 0.5 |
| Jan. 20, 22G | " | 2.6 | 6.9 |
| Jan. 5, 16G | " | 0.3 | 1.1 |
| Dec. 15, 22F | " | 1.3 | 2.1 |
| Nov. 3, N1 | NEN & DE | 0.7 | 0.8 |
| Mar. 17, 16F | " | 5.7 | 10.3 |
| Mar. 17, 22F | " | 4.0 | 4.6 |
| Feb. 16, 22F | " | 2.7 | 3.3 |
| Feb. 16, OBE | " | 2.4 | 2.3 |

| | | | | |
|---------|-----|----------|-----|-----|
| Feb. 3, | 30E | NEN & DE | 0.7 | 0.5 |
| Feb. 3, | OBE | " | 0.6 | 0.6 |
| Feb. 3, | 16F | " | 1.1 | 1.0 |
| Feb. 3, | 16G | " | 0.6 | 0.4 |
| Feb. 3, | ED | " | 0.8 | 0.8 |
| Feb. 3, | EE | " | 3.2 | 4.2 |
| Feb. 3, | 2F | " | 0.8 | 0.4 |
| Feb. 3, | N1 | " | 0.6 | 0.3 |

NEN - New England Nuclear
 BIO - Biokit
 DE - Diethyl ether

The replicate values were quite similar in most cases although there was an increase in variability for values less than 0.5 ng/ml. and greater than 4.0 ng/ml.. The increased variability at the lower end of the scale is due to the flattening of the standard curve in this area. In this area very slight differences in C.P.M. result in substantial differences in the calculated progesterone value.

However the magnitude of the observed variation, in all but one case (Jan. 5, 16G), was not great enough to alter the interpretation of the results. Values less than 0.5 ng/ml. would indicate a non-cycling animal and values greater than 4.0 ng/ml. would indicate ovarian activity. Also there was no consistent pattern in the differences between techniques. Therefore I considered that the progesterone values obtained in different assay runs and with changes in technique were com-

parable to each other.

Seven samples were reassayed after a chromatographic separation had been done to specifically extract progesterone. The chromatographic procedure was done exactly as described in the N.E.N. kit.

| Sample | Progesterone Value Without Chromatography (ng/ml.) | Progesterone Value With Chromatography (ng/ml.) |
|--------------|--|---|
| Oct. 24, 30E | 13.6 | 13.4 |
| Oct. 24, EE | 1.1 | 1.2 |
| Oct. 10, 16G | 0.9 | 1.5 |
| Dec. 1, OBE | 0.9 | 1.8 |
| Jan. 20, 2F | 0.7 | 1.3 |
| Oct. 10, OBE | 0.5 | 1.0 |
| Apr. 12, 22F | 5.7 | 2.0 |

The first 2 samples run through the column resulted in almost identical results to the assay without chromatography but subsequent samples were extremely variable. This suggests that the column may not have been rinsed sufficiently for the subsequent samples. However the high value for progesterone in the first sample confirms that the high values obtained in assays without chromatography were indeed progesterone and not cross-reacting compounds.

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