EFFECT OF NUTRITION ON GROWTH OF WHITE-TAILED DEER FAWNS

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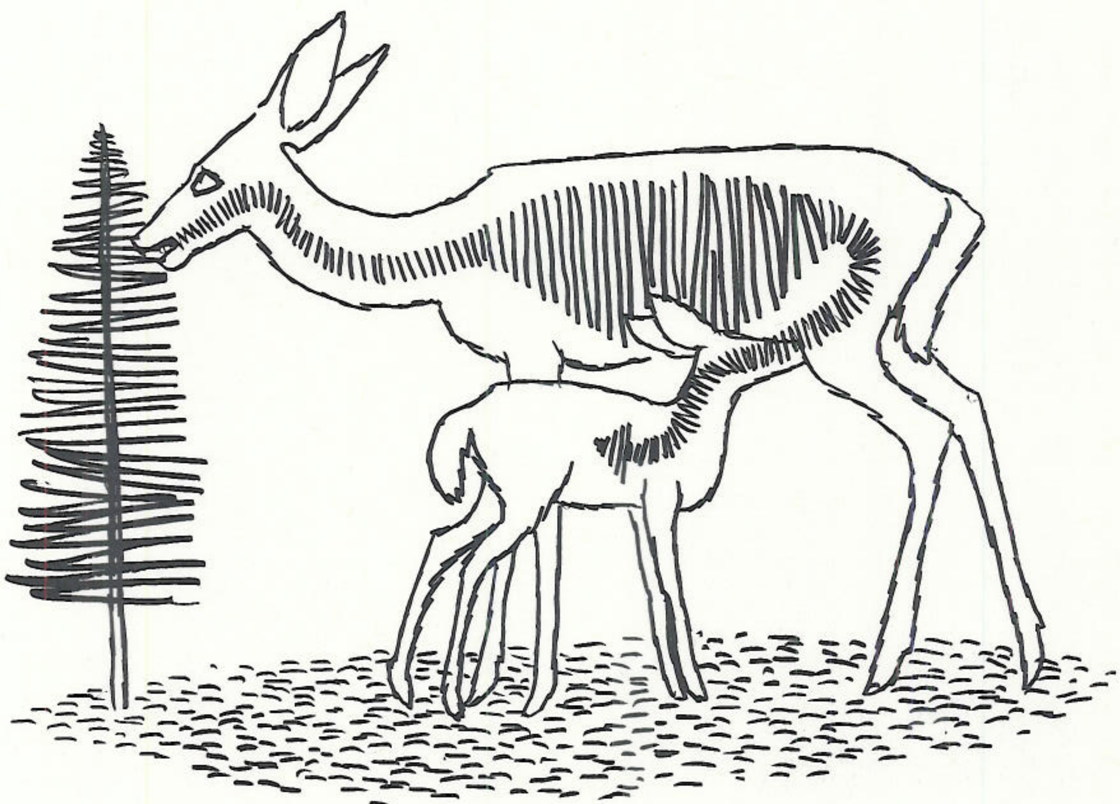

GAME DIVISION
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MICHIGAN
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Winter-spring nutritional combinations used to test the effects of different planes on pregnant deer are as follows:

Dietary Group	Winter Nutrition	Spring Nutrition
I	High	High
II	Moderate	High
III	Low	High
IV	Low	Moderate
V	Low	Low

Unquestionably, the relative degree of stress incurred by does increased in direct proportion to the decline in dietary plane. The effects of malnutrition were thus most pronounced for animals whose period of fasting extended into mid-spring -- the lower groups.

To correlate the mother's health status with that of her fawn, newborn young were promptly weighed and measured, and ear-tagged. Physical development, or size, at birth was ascertained by measuring the fawn's body length (top of nose to posterior tip of sacrum along the spine), hind foot (point of hoof to tip of calcaneum), ear span (apex to inner notch), and head width (groove behind postorbital process on frontal bone). Fawns were weighed on a dial scale to the nearest two ounces. Thereafter, I weighed them weekly until they were four weeks old. Beyond that age they were much too fleet afoot to capture without risk of injury. Primarily because of heavy natal and early post-partum losses, the number of fawns available for weighing declined slightly each week. A few animals were shifted to another phase of the study before they were a month old.

In addition, I obtained 97 fetuses, including 21 of known age, from experimental deer. These fetuses were mainly from does sacrificed for autopsy; however, a few mothers had starved in winter. To supplement this sample, I examined specimens from wild, road-killed does from the Cusino area. Most fetuses were inspected in fresh condition; a few were preserved in 10 per cent formalin. Forehead to rump (F-R) length in millimeters was measured on all fetuses. Weights of small fetuses were taken directly in grams; that of large specimens in ounces, later converted to grams. Approximate age of the fetus was determined according to the key in Armstrong (1950).

Influence of Nutrition on Fetal Development

Normal Growth Curve: To my knowledge no one has investigated whether fetal growth is influenced by physical condition of the mother. Conceivably, such relationships could be of considerable diagnostic value in predicting natal fawn mortality rates according to range carrying capacity. To ascertain the normal pattern, initially I constructed growth curves based on a total of 316 fetuses from northern Michigan does. Figure 1 presents the mean F-R lengths and body weights plotted by mid-point dates for 16 fetal age classes. For comparative purposes, growth curves of 21 known-age specimens (included in the composite sample) are shown separately. These fetuses were taken from does in excellent health when

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Effect of Nutrition on Growth of White-tailed Deer Fawns[1)]

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This paper presents the results of experimental studies to determine the effect of various nutritional levels in white-tailed deer (Odocoileus virginianus) on pre- and postnatal growth of the fawn. Most workers have appraised the fawn's status under situations of generally adequate rations for the mother (Nichol, 1938; Cowan and Wood, 1955; Haugen, 1959; and others). Since many Michigan deer are commonly subjected to severe physical stress in winter because of acute browse shortages and harsh weather, the need for comparative vital statistics is quite obvious. This investigation was conducted from 1954 to 1962 in Michigan's Upper Peninsula. In nine years I obtained reproductive records on 203 captive, pregnant does that produced 312 young.

I wish to thank Michigan Department of Conservation Game Division colleagues for valuable help in various phases of this project and report, especially H. D. Ruhl, R. A. MacMullan, D. W. Douglass, and D. F. Switzenberg, now retired.

Study Methods

Experimental layout, herd composition, and feeding regimen for this study were reported in detail earlier (Verme, 1962). To reiterate briefly, I maintained groups of adult does in small pens during winter and spring. In winter the animals were fed prescribed rations consisting principally of natural browse over a 100-day period which essentially corresponds to the typical deeryarding season in this region. By controlling the quantity and quality of food, I provided high, moderate, and low-value diets. Consequently, at the end of the trials, mean losses in body weight amounted to approximately 5, 16, and 26 per cent, respectively. In contrast to the excellent vigor of does on plentiful rations, by the end of the winter trials deer on extremely poor diets were very thin and weak from hunger.

In spring I switched the ration to Kellogg deer pellets and regulated the feeding of pellets to provide high, moderate, and low nutritional levels. To simulate natural food conditions, I raised the ration slightly at bi-weekly intervals during the spring. Differences in feed allotment among deer were greatest early in the season, but as time progressed the disparity gradually diminished. By mid-June, at the peak of fawning, all deer received the same ration, essentially a high level. In July the nursing does were fed all they would eat.

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Table 2 reveals that at respective stages the weights of an intact uterus and its single fetus are not consistently different between does in good and does in poor vigor. On the other hand, data for twins plainly show a sizable advantage, both in uterus and fetal weights, in favor of well-fed deer. Oddly, the fetus/uterus ratio ordinarily is much higher than normal among unthrifty deer, particularly for those with twins. The findings suggest to me that although other physiological factors may be involved, the uterine fluids may not be produced or maintained at regular levels among does subjected to malnutrition. Unfortunately, I did not measure the uterine fluids while removing the fetus.

Obviously, insufficient prenatal nutrition markedly slows the growth of fetuses so as to be readily measurable. The practical implications of these findings are considerable.

Size of Fawns at Birth

Dietary Plane and Fawn Size: Birth weights of 201 fawns (excluding 14 atrophic fetuses carried to term) from this study show an extreme range of from 2.0 to 10.1 pounds in which the average was 6.5 pounds. However, size of newborn fawns varied extensively, depending primarily upon dietary plans of the mothers. For example, mean weight of 67 fawns from high-diet Group I deer amounted to 7.8 pounds, as against 4.2 in 14 Group V young dropped by malnourished does (Table 3). Compared to Group 1 animals, fawns from Group II were 12 per cent lighter, Group III weights were 28 per cent lower, and fawns from Groups IV and V weighed 31 and 46 per cent less, respectively.

Moreover, skeletal growth of fawns also was inhibited by in utero nutritive deficiencies, although not to the same extent as weight. Hind foot (hock) length, probably the best indicator of frame development, varied from a mean of 10.7 inches in Group I fawns to 8.7 in Group V progeny, a difference of nearly 19 per cent. Measurements for body length, head width, and length of ear likewise confirm the fact that fawns born to impoverished does tend to be runty and emaciated.

Inevitably, a fawn's life expectancy closely hinges on its size at parturition. Examination of data for Groups III, IV, and V -- deer on low diets -- serves to illustrate this point. As the production of progressively smaller and lighter (from $\bar{x}$ = 5.8 pounds to 4.2) offspring increased, the respective mortality rates rose from 35 to 93 per cent of the crop (Verme, 1962). Surviving fawns averaged 6.4 pounds at birth, over 2 pounds heavier than those that died. Conversely, fully developed but stillborn young weighed only 3.3 pounds on the average as against 4.4 for progeny born alive but dying from nutritive failure within 48 hours. Finally, fawns dropped before the peak of parturition weighed 4.9 pounds and suffered 70 per cent casualties, compared to 5.8 pounds and 35 per cent mortality among those born later.

Although the rations were gradually raised to a high level in late spring, it is quite evident that dietary improvement came too late to help most of the underfed does. Experiments on sheep have conclusively shown that the pregnant ewe must receive a high plane of nutrition if she sacrificed. Fetal data for the average sample represent all stages of physical condition among mothers, from very good vigor to extremely poor. As expected, therefore, at respective stages in gestation the known-age specimens are slightly larger than average, especially near the end of the cycle.

With respect to the validity of Armstrong's (1950) aging criteria, I concur with Palmer (in op. cit.) that the key tends to underage some fetuses. Although I lack definite proof, in my opinion the pace at which external features evolve is largely independent of the fawn's relative vigor (except, perhaps, when death of the fetus or mother is imminent). This contention is basic to the interpretation of findings in the following discussion.

Weight Variations of Fetus and Uterus: Like other animals, most of the growth of the deer fetus takes place in the last third of gestation. Clearly, the quantitative demands for nutritive materials in the mother are rather small at first, but they progressively increase to become several times as large toward the close of the period (Maynard and Loosli, 1956). Pregnancy is known to increase the need for protein much more than the need for energy. If the diet is inadequate in all respects, the mother sacrifices her bones and body tissue to nourish her fetus. After a prolonged siege of malnutrition and bitter cold weather, however, the doe's reserves may be small or non-existent (Kitts, et al., 1956). If this is true, the fetus might be radically affected by insufficient essential nutrients as it approaches term.

To check this assumption, I sorted the autopsy records for does which carried fetuses at least 121 days old, with respect to the mother's relative vitality as time of death. Deer that had appreciable internal fat and a femur fat content of at least 50 per cent (Cheatum, 1949) were assigned to a good vigor class. Does whose health index fell below these standards were placed in a poor group. In experimental deer, recourse to body weight data provided a factual basis for appraising physical condition.

Altogether, 137 fetuses were old enough to be suitable for this analysis. Examination of Table 1 reveals that at about 133 days' gestation, inadequate nutrition begins to retard fetal development. Beyond this time, growth in length and (primarily) weight of fetuses from impoverished does falls rapidly behind that of normal young. At approximately 151 to 180 days, for instance, differences in F-R length and weight between good and poor fetuses amount to about 30 millimeters and 830 grams, respectively. Interestingly, size differences in the final 20 days of gestation are less pronounced. However, no fetuses from half-starved penned deer are present in this age group, in contrast to appreciable numbers of such specimens in the younger classes.

Concurrent with this work, I weighed unopened uteri from pregnant does to determine the relation of total biomass to that of fetuses inside. This was done by severing the reproductive tract at the cervix and cutting away connective tissue and ligaments. By means of the scheme described earlier, I segregated the data for 44 does in the last third of pregnancy.

Primarily because of heavy natal mortality, surviving Groups III, IV, and V fawns were considerably larger than average (see Table 3). Still, I doubt that natural selection, in which unfit specimens were ruthlessly weeded out, entirely explains the situation of very rapid growth among surviving fawns. It should be emphasized that although food allotment was raised throughout the parturition season, many Groups I and II offspring were born before the mother's ration was at a high level. In contrast, most early-born Groups III to V fawns died; hence, most of those that lived were dropped after the peak partum date.

Perhaps most important, Groups I and II deer nursed an average of 1.58 fawns per doe during the first month, as compared to 1.32 young each for mothers in Groups III-V. While nearly 60 per cent of the high-diet does reared twins, only a third of the mothers on poorer levels nursed two fawns. Consequently, Groups I and II mothers were commonly saddled with early-born progeny, larger fawns, and more of them. Under these circumstances, the heavily burdened lactating doe may not have been able to produce sufficient milk, in terms of pounds of milk per pound of fawn, to properly suckle her offspring.

As stated above, small fawns grow proportionately faster than very large newborn young. Analysis of relative growth rate, presented in Figure 2, is based on continuous data for the 116 fawns available throughout the weighing period. The appraisal is in relation to eight birth classes (3.0-3.9 pounds, 4.0-4.9 . . . 10.0-10.9), combining similar data for all dietary groups. Evidence of growth variations due to birth size is gleaned from the fact that small, medium, and large fawns ($\bar{x}$ = 3.8, 6.5, 9.4 pounds), respectively increased 4, 3, and 2½ times in weight during the initial four weeks. Yet, despite a tendency toward compensatory growth among originally small individuals, the final weight span was still considerable (Figure 2).

These findings probably represent a natural growth phenomenon; e.g., compared to undersize newborn young, it might be physically impossible for extremely big fawns to make a four-fold weight increase in one month. As shown by Table 5, most of the smaller, hence faster-growing fawns were produced by deer in Groups III to V. The operation of this factor in concert with other variables mentioned undoubtedly explains the seeming contradiction in pattern of growth response manifested by fawns per dietary group.

<u>Effect of Litter Size and Sex on Growth</u>: Surprisingly enough, relative growth rate was slightly slower for single fawns than for twins; however, fawns from one birth were somewhat larger to start with, and at four weeks old. Single fawns reared by 2-year-old does grew a shade faster than those nursed by prime-age mothers, but they were born smaller and generally dropped later. The best weight gains were made by the lone survivor from a multiple litter decimated by heavy infant mortality. This is expected, since a physically mature mother dropping twins or triplets certainly is capable of nursing her sole living fawn at an optimum level.

is to produce large, healthy lambs of which few die, in contrast to the weak, small lambs and high losses that result when ewes are improperly fed (Thomson and Thomson, 1948, 1953; Wallace, 1948).

Relation of Natural Factors: As a rule, a single fawn is approximately a half-pound heavier at birth than one of twins (Table 4). The spread in weight tends to widen progressively from Group I to Group IV. Naturally, a poorly-fed doe carrying twins is much more hard-pressed to provide even minimal sustenance compared to a mother with one fetus. This is tellingly illustrated by the fact that Group I twin fawns were more than twice as heavy at birth as those in Group V, compared to 75 per cent greater weight of a Group I single fawn over a Group V single.

Fawns from multiple litters often vary appreciably in size. Thus it seems reasonable to conclude that as prenatal stress intensifies there may be an unequal division of nutrients among individuals. Perhaps this physiological tendency enables one fawn to be salvaged when the probability that both young will survive is very remote. Since Group V newborn twins did not differ substantially in size, however, there is an indication that when a doe reaches a crucial level in physical condition, inequality in growth probably is unimportant as both progeny are doomed.

Collectively, data for 92 males and 109 females show no consistent differences in weight for all litters (1, 2, and 3 fawns). Among 66 singles, the average female was somewhat heavier than the male; however, nearly half of the females were exceptionally large Group I individuals. On the other hand, mean birth weights for 126 twin fawns definitely favor males over females by nearly a half-pound. To some degree, the weight differential increases slightly from Group I on, a possible suggestion of innately better resistance to prenatal hardships among males.

Single fawns produced by 2-year-old versus prime-age (3 to 7 years) does did not differ substantially overall. Within a dietary group, however, the average individual from older mothers ranges from a few ounces to over a pound heavier. In general, the size spread increases as the plane of nutrition declines. This is entirely logical and understandable; compared to older deer, 2-year-old does are still physically immature. Consequently, young mothers probably are much more vitally affected by chronic food shortages, especially during late pregnancy.

Early Postnatal Growth of Fawns

Growth Rate and Dietary Plane: Inspection of Table 5 suggests a small paradox: Postnatal growth rate of fawns in this study is inversely correlated with the dietary level of the doe. For example, Group I progeny averaging nearly 8 pounds at birth grew to about 21 pounds in four weeks, an increase equal to 2.67 times original size. Concurrently, Group III fawns increased from 6.4 to 20.4 pounds, or 3.19 times the original size. Since fawns in other dietary groups also manifested differential growth, despite the initial spread, the weight difference ceased to exist at four weeks for all practical purposes.

Summary

Experimental feeding trials were conducted on penned, pregnant does in winter and spring to determine the effect of various dietary planes on pre- and postnatal development of whitetail fawns. Malnutrition in the mother results in retarded length and weight growth of her fetus beginning at about 133 days' gestation. At birth, fawns from nearly starved mothers average about 46 per cent lighter, and they tend to be stunted skeletally, compared to young from well-fed does.

Early postnatal growth rate in fawns in this study was inversely related to the does' earlier nutritional status. In contrast to malnourished deer, properly-fed mothers incur a proportionately greater lactation burden because they have bigger young, suckle more twins, and successfully rear their early-born offspring. Initially tiny fawns experience a faster, or compensatory, rate of growth compared to very large young. Hence, despite the original disparity in weights, because of the coaction of various biological forces, the size gap may be practically non-existent at four weeks old. Fawns grow very rapidly and most of them roughly tripled in weight in the first month.

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Although mean birth weights of 51 male and 65 female fawns were virtually identical, in one month the males were nearly a half-pound heavier. Single males grew a bit faster than single females which were larger initially. On the other hand, among mixed twins the females led in rate of gain by a scant margin. This indicates that the bigger, and perhaps more aggressive, males do not necessarily get the lion's share of the mother's milk. Nevertheless, I commonly observed that one individual of twins promptly outstrips its litter mate in growth, hence in ultimate size, even though their starting weights were similar.

Lactation Stress and Fawn Metabolism

Growth of whitetail fawns closely resembles that noted for black-tailed deer (O. hemionus columbianus) by Cowan and Wood (1956). The average fawn in this study gained nearly a half-pound per day during the first month, although the rate of increment was slightly greater among large fawns. During their second week, most fawns experienced rather sharply reduced growth; however, the normal pace was quickly recovered (Figure 2).

When about two weeks old, fawns begin eating solid food, which may enable them to offset a possible shortage of milk. Actually, I strongly doubt that milk yield varied appreciably with respect to the doe's earlier dietary status. However, Thomson and Thomson (1953) report that milk yield of the ewe is closely dependent upon her nutritional level during late pregnancy and during lactation. Chemical analysis of milk samples from does in this study likewise failed to reveal differences in constituents that could be directly related to winter and spring nutritional levels (Verme, Youatt, and Ullrey, 1962). Plainly, if the doe gets sufficient food to support lactation, her milk will be of excellent quality; thus, the fawns will make extremely rapid growth.

From their hungry behavior, many does suffered from physiological stress during the second week of lactation, particularly if the young were dropped early. In the first three weeks of lactation, the mother's blood picture shows little if any improvement, or it may deteriorate slightly (Verme, Youatt, Ullrey, op. cit.). Ordinarily, heavily-producing deer lose some body weight during this period, particularly those rearing twins. As in the case of the cow (Maynard and Loosli, 1956), it frequently is impossible to get the nursing doe to consume enough food to compensate for her total energy expenditure.

Kitts, et al. (1956) postulate that inadequacies in lactation because of earlier malnutrition in the doe may increase postnatal mortality because the fawn's normal growth is impaired. Similarly, Cowan and Wood (1955) suggest that a temporary setback in the fawn's growth due to unusual circumstances may sometimes lead to relatively major upsets in the regular pattern. However, I see no indication that a brief nutritional disorder critically affects the health of fawns. The nursing doe and her progeny are remarkably hardy animals and they are inherently resistant to environmental pressures. There is little evidence that Michigan's summer range ordinarily is limited in quality or quantity in browse. Nevertheless, the great value of lush-quality habitat is quite apparent. Drastic food shortages in other seasons are much more important in controlling the biology and population dynamics of deer.

TABLE 1

Relation of Fetal Development to Physical Condition of Does

Gestation Age Class (Days)	Physical Condition of Does[1]	Fetuses Examined	Mean F-R Length (mm.)	Mean Weight (grams)	Growth Factor[2]
121-132	Good	14	304	823	2.50
	Poor	20	312	810	2.53
133-150	Good	18	345	1360	4.67
	Poor	25	342	1101	3.77
151-180	Good	8	410	2410	9.88
	Poor	28	379	1579	5.98
181-200	Good	14	447	2851	12.74
	Poor	10	440	2543	11.19

1) See text for method of determining physical condition.

2) Arbitrarily computed as length x weight x 10^{-5}

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TABLE 3

Mean Birth Weight and Skeletal Size of Fawns[1]

Dietary Group	Fawns Examined[2]	Weight (Pounds)	Body Length	Head Width	Ear Span	Hind Foot
I	67	7.8 ± 1.2[3]	24.1	2.22	3.32	$10.7 \pm .6$
II	49	6.8 ± 1.2	22.5	2.19	3.27	$10.3 \pm .6$
III	36	5.8 ± 1.6	21.6	2.15	3.21	$9.9 \pm .7$
IV	35	5.4 ± 1.9	21.4	2.14	3.13	9.5 ± 1.0
V	14	4.2 ± 1.2	19.9	2.10	2.86	$8.7 \pm .8$
Means and Total	201	6.5 ± 1.4	22.5	2.18	3.22	$10.1 \pm .7$

1) See text for manner of measuring skeletal size; data are in inches.

2) Excluding 14 dead fetuses carried to term.

3) Standard deviations

TABLE 2

Effect of Doe Physical Condition on Fetus and Uterus Weights[1]

Gestation Age Class (Days)	Physical Condition of Doe[2]	Uteri Examined	Mean Weight Single Uterus	Mean Weight Single Fetus	F/U Ratio	Uteri Examined	Mean Weight Twin Uterus	Mean Weight Twin Fetuses	F/U Ratio
121-132	Good	3	2363	756	.320	3	4120	1607	.390
	Poor	2	2211	836	.378	2	3742	1389	.371
133-150	Good	1	3175	1049	.330	5	5807	2682	.462
	Poor	3	2344	1002	.427	7	3986	2075	.521
151-180	Good	1	4028	1928	.479	3	9223	5160	.559
	Poor	2	3772	1375	.365	6	5670	3298	.582
181-200	Good	2	5330	3233	.607	1	12587	6922	.550
	Poor	1	6917	4423	.639	2	8051	5051	.627

1) Weight of unopened uteri and fetuses in grams

2) See text for method of determining physical condition.

TABLE 5

Growth Rate of Fawns

Dietary Group	Birth	7 Days	14 Days	21 Days	28 Days	Rate of Gain
	Mean Weight Pounds					
I	7.9 ± 1.3[1] (60)[2]	11.7 (60)	14.1 (54)	17.6 (51)	21.1 ± 2.7 (49)	2.67
II	6.9 ± 1.3 (45)	10.5 (45)	13.3 (38)	16.5 (37)	19.8 ± 2.9 (34)	2.87
III	6.4 ± 1.3 (23)	10.6 (23)	13.5 (23)	17.1 (22)	20.4 ± 2.1 (16)	3.19
IV	6.3 ± 1.7 (19)	9.9 (17)	12.9 (19)	16.8 (16)	19.9 ± 2.6 (16)	3.16
V	5.8 (1)	9.9 (1)	14.0 (1)	17.6 (1)	21.5 (1)	3.71
Means and Totals	7.1 ± 1.5 (148)	10.9 (146)	13.6 (135)	17.1 (127)	20.4 ± 2.8 (116)	2.87

1) Standard deviation

2) Numbers of fawns examined are shown in parenthesis.

TABLE 4

Influence of Number in Litter on Fawn Weight

Dietary Group	One Fawn	Two Fawns	Three Fawns
	Mean Weight (Pounds)		
I	8.4 (20)[1]	7.8 (41)[2]	6.3 (6)
II	7.3 (13)	6.7 (36)	
III	6.3 (15)	5.4 (21)	
IV	6.8 (10)	4.8 (22)	5.1 (3)
V	4.8 (8)	3.5 (6)	
Means and Totals	7.0 (66)	6.4 (126)	5.9 (9)

1) Numbers of fawns examined are shown in parenthesis.

2) In four sets, one twin was atrophic and therefore not weighed; thus, the number of fawns is not always devisable by two.

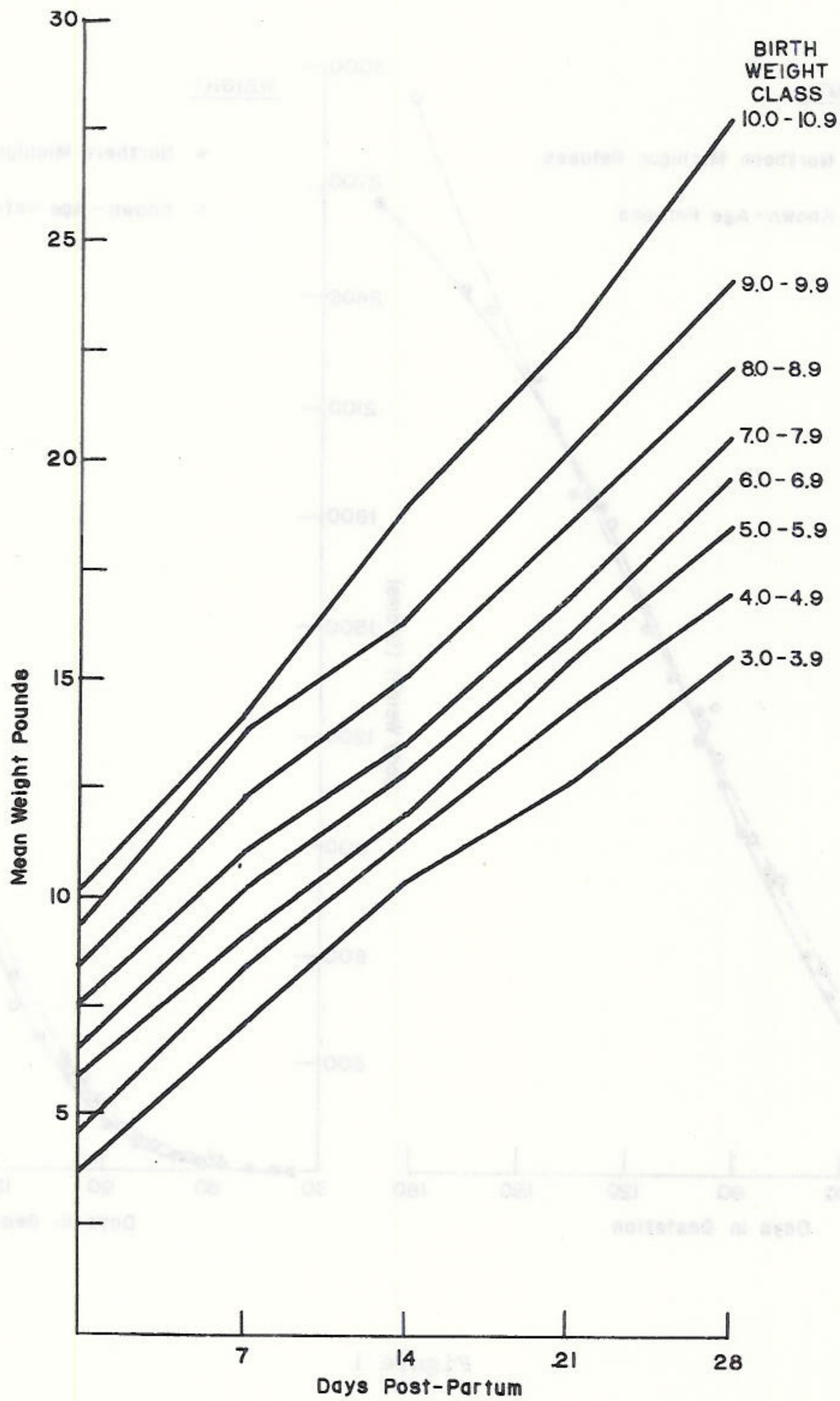

Figure 2

Relative growth and rate of weight gain according to birth weight class of fawns

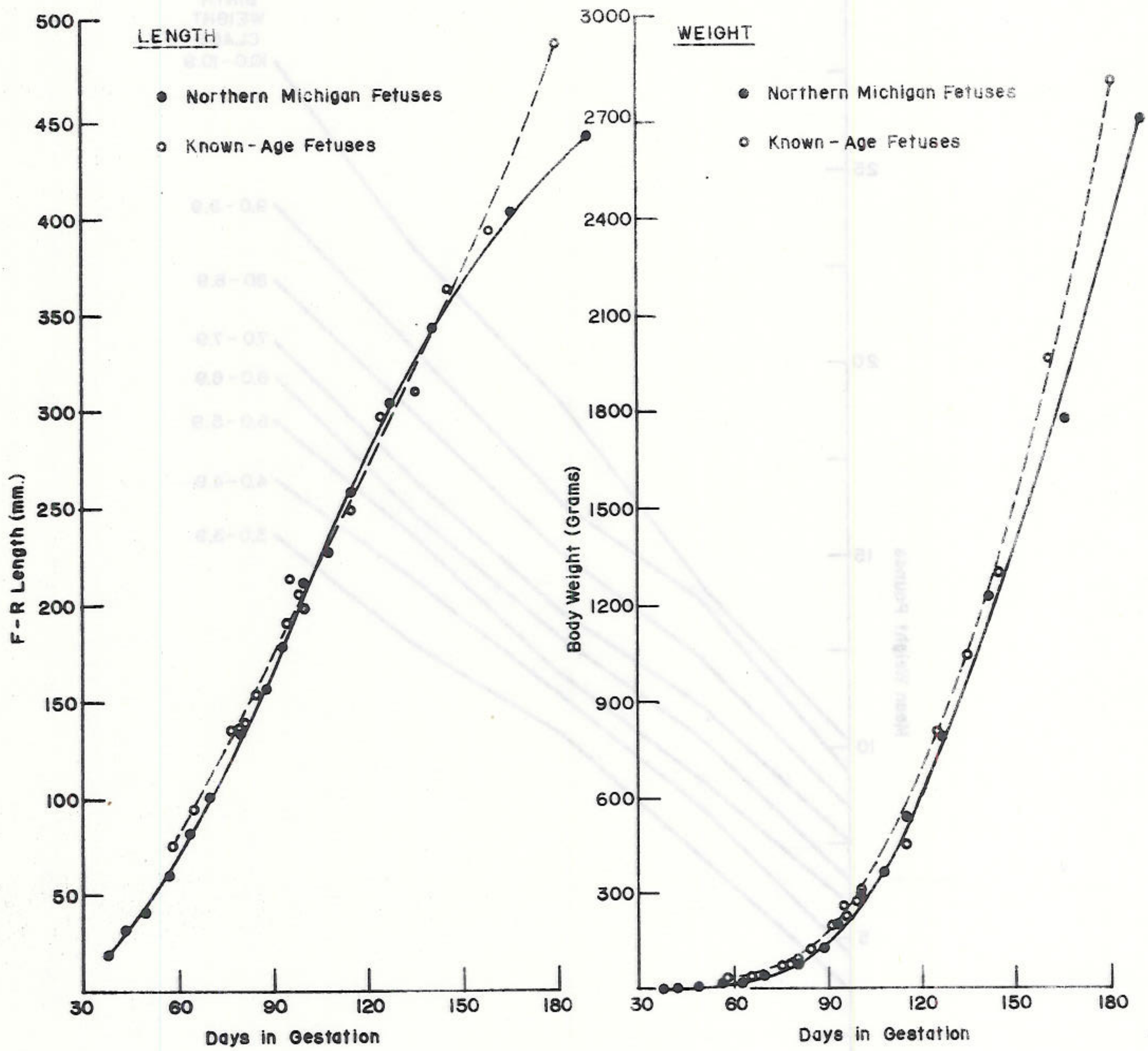

Figure 1

Growth curves for 316 Northern Michigan fetuses compared to 21 known-age specimens; curves eye-fitted