DEVELOPMENT OF THE COLUMBIAN BLACK-TAILED DEER

(ODOCOILEUS HEMIONUS COLUMBIANUS)

DURING THE FETAL PERIOD

by

PETER D. OMMUNDSEN

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Department of Zoology

The University of British Columbia
Vancouver 8, Canada

Date May 15, 1967

ABSTRACT

A series of 88 fetuses of the Columbian black-tailed deer (Odocoileus hemionus columbianus) was examined and measured. From the data obtained it was possible to reconstruct the probable sequence of changes in morphology and patterns of relative growth that occur during the development of the fetus. A series of stages of development was outlined, based on external morphological characteristics.

The auricles of the ears appear to be the fastest-growing structures in relation to body length. The cranial portion of the skull grows in diameter faster than the inter-orbital region. In length, the preorbital and postorbital segments of the skull show similar growth rates. The neck grows in circumference relatively faster than the abdomen. The hind limbs grow faster than the fore limbs. Greater differences in patterns of relative growth were observed between this subspecies and the Northern white-tailed deer (O. virginianus borealis) than between the black-tailed deer and Rocky Mountain mule deer (O. h. hemionus).

Some sources of variation were examined, including technical problems, individual differences, differences between

the sexes and the relationship between size and form. Not all regions appear to develop at the same rate in different animals. Males were found to be larger than females at the same stage of morphological development. Some body dimensions had a much higher correlation with structural change than did others.

TABLE OF CONTENTS

	PAGE
ABSTRACT	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
ACKNOWLEDGEMENTS	viii
INTRODUCTION	1
MATERIALS AND METHODS	4
1. Fetal Material	4
2. Collection of Material	5
3. Methods of Preservation	6
4. Examination of External Form	7
5. Method of Designating Levels of Structural Development	7
6. Measurements	8
7. Weights	15
RESULTS	16
A. Evaluation of Methods	16
1. Sources of Material	16
2. Evaluation of External Dimensions	20
3. Effects of Preservation on Results	23

	PAGE
B. General Description	28
1. Vibrissae and Pigment Patterns	28
2. Outline of External Development	30
3. Patterns of Growth	57
C. Variability During Development	65
1. Differential Development of External Features	65
2. Development of Twins and Triplets	74
3. Sex Differences	74
4. The Relationship Between Size and Form	78
DISCUSSION	81
1. Technical Problems in Studying Development	81
2. Fetal Material	82
3. Patterns of Development	84
4. Variation in Development	89
LITERATURE CITED	94
APPENDIX	98

LIST OF TABLES

TABLE	PAGE
I. Measurements of a Series of Fetuses before and after Preservation in Formol Saline	25
II. Patterns of Growth in the Fetal Period of the Relationship $Y = b X^k$ where X Represents Forehead-rump Length	62
III. Patterns of Growth in the Fetal Period of the Relationship $Y = b X^k$ where X Represents Calcaneus-hoof Length	63
IV. Comparison of Fetal Growth Patterns in Three Forms of Deer	64
V. Comparison of Development in Ten Different Regions	72
VI. The Relationship between Size, Sex and Morphological Development in a Series of Fetuses	77
VII. Degree of Correlation between the State of Morphological Development and Various Dimensions	79

LIST OF FIGURES

FIGURES		PAGE
1 - 18	Growth Relative to Forehead-rump Length	99 - 116
19 - 35	Growth Relative to Calcaneus-hoof Length	117 - 133
36 - 38	Growth of the Head Region	134 - 136
39 - 41	Growth of the Trunk	137 - 139
42 - 44	Growth of the Limbs	140 - 142

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INTRODUCTION

The Columbian black-tailed deer (Odocoileus hemionus columbianus) inhabits a narrow strip on the Pacific slope of North America from Rivers Inlet, British Columbia to Monterey County, California (Cowan and Guiguet, 1965; Cowan, 1956). It is an important form of wildlife in this area and an understanding of its reproductive biology is important to its management. This is an investigation of the prenatal development of that subspecies.

Although numerous workers have studied postnatal growth of deer, much less attention has been given to the prenatal period. According to Meyer (1936), William Harvey (1578-1657) dissected pregnant red deer (Cervus elaphus), Fallow deer (Dama dama) and roe deer (Capreolus capreolus). During the 19th century, observations on prenatal deer included those of Pockels, Ziegler and Bischoff. Th. Bischoff probably made the most systematic investigation of the century in his studies on roe deer in 1843. Schufeldt (1891) published observations on reindeer (Rangifer tarandus) fetuses, and Petrov (1964) studied the intra-uterine development of elk.

A number of investigations have been conducted on the genus Odocoileus. Cheatum and Morton (1942, 1946) established

a prenatal growth curve for the Northern white-tailed deer (Odocoileus virginianus borealis). Armstrong (1950) studied the fetal development of the same subspecies and characterized different ages of fetal life. Hudson and Browman (1959) published the results of a previous study by Hudson (1956) on the development of the embryo and fetus of the Rocky Mountain mule deer (Odocoileus hemious hemionus). Developmental characteristics were related to fetal age. Other studies on prenatal Odocoileus include the contributions of Segelquist (1966) and Nellis (1966).

The current investigation treats only the period of the fetus. There is little agreement regarding methods of defining the divisions between the periods of prenatal life. Generally, the embryonic period can be considered as one of differentiation and organization, including the development of the major organ systems. The fetal period is one of growth, with minor differentiation of external features. In this case, the fetal period was arbitrarily designated to include the smallest animal available for study in which most of the external features represented in the adult (hoofs, ears, etc.) were discernible. This was an animal with a crown-rump length of 24.2 mm.

The objectives of this investigation were:

1. To describe the changes in morphology that occur during the development of the fetus.
2. To describe the changes in size and the patterns of relative growth that occur during the fetal period.
3. To establish a series of stages of development based on external morphological criteria.
4. To evaluate sources of variation in fetal development.
5. To outline some technical procedures in studying development.
6. To compare the fetal development of this subspecies with that of other forms.

MATERIALS AND METHODS

1. FETAL MATERIAL

A total of 88 fetuses of Columbian black-tailed deer were available for study. These consisted of 23 singletons, 31 sets of twins, and one set of triplets. A group of 84 animals of determinable sex was made up of 38 females and 46 males.

Specimens of unknown age are distributed in time, in terms of date of collection, as follows:

1. Animals collected at Goldstream, Vancouver Island, British Columbia.

1940 January One singleton and one set of twins.

2. Animals collected at Shellburn, British Columbia.

1943 April One singleton.

3. Animals collected at Northwest Bay, Vancouver Island.

1964 January Four singletons and one set of twins.

February Two singletons and two sets of twins.

March Two singletons, seven sets of twins, and one set of triplets.

May Four singletons and eleven sets of twins.

June Two singletons and four sets of twins.

1965 January Two sets of twins

1966 April Five singletons and one set of twins.

May Two singletons.

Known-age animals were obtained from the University of British Columbia Wildlife Research Unit. One set of twins was collected in January 1966 and another set was collected in February 1966.

2. COLLECTION OF MATERIAL

Known-age specimens were obtained by sacrificing does at predetermined times after breeding. A 1½-year-old doe, a 2½-year-old doe and a 1½-year-old buck were available for breeding purposes at the University of British Columbia Wildlife Research Unit. The antlers were removed from the buck to prevent serious injury to the does. The breeding pen used was 20 feet long and 12 feet wide, with a partition extending lengthwise from the center of one wall for a distance of about eight feet. The does were exposed to the buck once every day from the last week of October 1965, until the second week in December 1965. The procedure was to introduce the does, separately or together, into the breeding pen, then introduce the buck and observe the animals constantly while together in the pen.

Between exposures, each animal was kept in a separate pen 20 feet long and four feet wide. The deer were fed a protein supplemented cereal ration, Buckerfields U.B.C. 3657, and

the food consumption of each animal was recorded daily. The animals were weighed at one-week intervals. The 1½-year-old doe was sacrificed on 18 January, 1966 and the 2½-year-old doe was sacrificed on 28 February, 1966.

Fetuses of unknown age collected during 1964, 1965 and 1966 from wild pregnant does were shot at Northwest Bay, Vancouver Island, British Columbia. The animals were collected from the Coastal Western Hemlock and Coastal Douglas-fir Zones of the Pacific Coastal Mesothermal Forest Region (Krajina, 1965).

3. METHODS OF PRESERVATION

Fetuses were preserved on dry ice, in an electric freezer, or in formol saline within several hours of the death of the doe. Material stored on dry ice was placed in electric freezers or formol saline within several days. No material was stored in electric freezers for more than five months before being stored in formol saline.

Animals with a forehead-rump length greater than 300 mm. had their abdomens opened with a small slit to allow faster penetration of the preservative. Formol saline was injected into the body cavities of some of these fetuses.

4. EXAMINATION OF EXTERNAL FORM

Every fetus was given a careful external examination, and all observations were recorded on data sheets. Information was collected regarding external morphological characteristics such as general body form and proportions, flexion, thickness of the integument, emergence of vibrissae, emergence of hair, hair patterns and hair colours, pigmentation of the skin, structure of the eyelids and preorbital gland, condition of the auricles of the ears and external auditory meatuses, structure of the mouth, tongue and teeth, condition of the external nares, external form of the brain and skull bones, condition of the antler primordia, structure of the genital organs, skin glands and limbs.

Observations were made using a 10-power hand lens and a dissecting microscope with a maximum magnification of 84X.

5. METHODS OF DESIGNATING LEVELS OF STRUCTURAL DEVELOPMENT

For the purposes of this study, several terms are used to facilitate discussions comparing the extent of morphological development between animals (assessed in terms of morphological appearance, without regard to size).

Rank is a numerical estimate of the level of development of an individual compared to any other individual.

Single-trait rank is the numerical level of structural development of one individual relative to others, with regard to one specific characteristic.

Mean rank is a numerical estimate of the overall relative level of structural development of an individual. This is the mean of the single-trait ranks of that individual.

Stage is a characteristic period during development. At a given stage of development, a fetus has a specific set of morphological characteristics. A stage refers to a period in the total developmental sequence of the fetus. A rank, conversely, is merely a rating device for comparing the relative levels of development of animals in a group.

6. MEASUREMENTS

A series of linear and circumferential measurements was taken on each fetus and recorded on data sheets. All measurements were recorded to the nearest .1 mm. In order to maintain uniformity of results, each animal was placed in the same position before being measured. It was placed on its right side, on

a flat surface with its back along a straight line, away from the examiner, and its legs extended. The head was prevented from curling backwards. All measurements were taken using reference points that could be located externally. No dissection was required.

The measurements used were chosen for several purposes:

1. To determine the accuracy with which each could be taken.
2. To provide data on the growth patterns of the species.
3. To study the effects of preservative fluid.
4. To evaluate the use of each measured attribute as an index of development.
5. To assess their value in field work.
6. To permit comparison of data with that of previous investigators.

All of the following measurements were tested. Some were very difficult to obtain with reasonable precision and were soon discontinued.

LINEAR MEASUREMENTS

These are measurements of straight distance between two structural points, taken with a vernier caliper, steel calipers, and a meter stick.

General

1. Crown-rump length is the distance from the top of the mesencephalon hump to the posterior end of the animal.
2. Forehead-rump length is the distance from the area of intersection of the coronal and sagittal sutures to the tuberosity of the ischium.

Head

1. Head length is the distance from the tip of the nose to the lamboidal crest.
2. Head height is the distance from the lateral side of the incisors to the lamboidal crest.
3. Face height is the distance from the base of the chin to a projected line joining the inner corners of the two eyes.
4. Diameter at nares is the transverse diameter of the head taken at the posterior end of the external nares.
5. Mouth breadth is the straight distance between the two corners of the mouth with the lips closed.
6. Interocular breadth is the distance between the right and left entocanthion.
7. Diameter of orbit is the distance between the ectocanthion and entocanthion.

8. Bizygomatic breadth is the breadth of the skull directly in front of the ears.
9. Biauricular breadth is the straight distance between the right and left ear notches.
10. Ear length is the distance between the proximal notch and the tip of the ear, taken with the auricle held along the vertical plane of the head.
11. Ear width is the greatest width of the auricle, taken with the auricle held along the longitudinal plane of the head.
12. Preoptic length is the distance from the tip of the nose to the entocanthion.
13. Postoptic length is the distance from the ectocanthion to the proximal notch of the ear.
14. Cranial length is the diameter of the orbit plus the post-optic length.

Trunk

1. Total spine length is the distance from the lambdoidal crest to the tip of the tail, excluding hairs.
2. Precaudal spine length is the distance from the lambdoidal crest to the posterior end of the sacrum.
3. Shoulder point to pin bone is the distance from the metacromion process of the scapula to the tuberosity of the ischium.

4. Shoulder point to hip bone is the distance from the metacromion process of the scapula to the crest of the ilium.
5. Withers to tail head is the distance from a point mid-way between the vertebral borders of the two scapulae to the posterior end of the sacrum.
6. Hip bone to pin bone is the distance between the crest of the ilium and the tuberosity of the ischium.
7. Shoulder breadth is the distance between the metacromion process of each scapula.
8. Neck length is the distance from the metacromion process of the scapula to the atlas.
9. Transverse chest diameter is the transverse diameter of the chest directly behind the forelegs.
10. Sagittal chest diameter is the depth of the chest in the mid-sagittal plane directly behind the forelegs.
11. Dorsal tail length is the distance between the tip and head of the tail.
12. Ventral tail length is the distance between the tip of the tail and the ventral junction of the tail and rump.
13. Hip width is the distance between the crests of the two ilia.
14. Bitrochanteric diameter is the distance between the right and left femoral trochanters.

Limbs

1. Length of humerus is the distance from the proximal side of the greater tuberosity to the posterior side of the olecranon process.
2. Length of foreleg is the distance from the olecranon process to the hoof point.
3. Length of forefoot is the distance between the hoof point and the posterior junction of the foot to the leg.
4. Length of femur is the distance from the greater trochanter to the patellar flexure.
5. Length of hind leg is the distance from the tubercle of the tibiofibula to the hoof point.
6. Length of hind foot is the distance from the tip of the calcaneus to the hoof point.
7. Calcaneus-hoof length is the distance from the tip of the calcaneus to the distal edge of the proximal bevel of the hoof.

CIRCUMFERENTIAL MEASUREMENTS

These measurements are taken by passing a thread around the structure concerned and then measuring the length of the thread with vernier calipers or a meter stick. Each measure-

ment was taken three times and a mean obtained for the final result.

General

1. Contour length is taken from the tip of the nose between the external nares to the tip of the tail.

Head

1. Head width is taken from the posterior corner of one eye, over the cranial dome to the posterior corner of the other eye.
2. Horizontal head circumference is taken around the base of the smooth prominence of the forehead, above the eyebrows and in front of the ears.
3. Vertical head circumference is the distance around the cranial dome across the posterior corner of each eye.
4. Mouth cleft length is taken between the two corners of the mouth along the lips.
5. Head contour length is the contour of the head from the tip of the nose to the lambdoidal crest.

Trunk

1. Median neck circumference is taken at a point mid-way between the metacromion process of the scapula and atlas.

2. Chest circumference is taken directly behind the forelegs.
3. Abdomen circumference is taken at a point immediately anterior to the umbilical cord.

7. WEIGHTS

The total body weight was obtained for each fetus. All were weighed after formol saline preservation. Some were weighed when fresh as well as at intervals after being stored in preservative to test for changes. All animals were dried with paper towels before being weighed. Fetuses weighing less than 500 grams were weighed to .1 gram on a Mettler electric balance. Those weighing more than 500 grams were weighed to the nearest gram on an Avery pan balance.

RESULTS

A. EVALUATION OF METHODS

The information derived from the animals used in this investigation is probably not completely representative of fetal development in wild Columbian black-tailed deer. Before these data may be compared to those of other investigators, past or future, careful consideration must be given to the techniques and material selected in each case. This evaluation of methods is a discussion of useful results including possible sources of bias, sampling error and lack of accuracy.

1. SOURCES OF MATERIAL

Two sets of twin fetuses of known age were obtained after breeding one buck to two does. Cultivating useful material for an investigation on prenatal development is an important and time-consuming procedure. It is possible that such factors as the size, age and parity of the parents, as well as the conditions under which they are bred and reared, may influence the development of the fetuses (Hafez, 1963).

Information obtained from the breeding procedure described here may be useful in helping to control such conditions.

Behavior during the days prior to mating

At the outset of the breeding program it was planned that the buck and two does be placed together in the breeding pen for at least three hours daily. The placing of all three animals in the pen together was soon judged to be unsatisfactory, as the 2½-year-old doe was very aggressive towards the other two animals. Consequently, the procedure was changed so that only one doe at a time was allowed in the pen with the buck.

When the buck, antlers removed, was introduced to the 1½-year-old doe in the breeding pen, the following pattern of behavior was always observed. When first placed together, the buck would sniff the doe and rub his muzzle along her back. Within a few minutes he would begin exhibiting aggressive behavior, typically the crouch and snort described by Cowan and Geist (1961). Following this, the buck would rush and chase the doe for variable periods of time. If allowed to remain together, the chasing would subside and the animals would lie down. Usually the entire pattern would then be repeated. The animals were not left together for three hours daily as was originally planned due to the risk of injury to the doe from

the attacking buck or from trying to avoid him. After the first week of the project they were rarely allowed to remain together for more than 10 minutes.

When the buck was introduced to the 2½-year-old doe, she typically ran wildly in the pen, frequently attacking the buck by "striking," a behavior pattern described by Thomas et al. (1965). Consequently, the animals were rarely allowed to remain together in the breeding pen for more than 10 minutes daily.

No difference was apparent in the behavior patterns described if the buck was allowed to enter the breeding pen before the doe, if the doe entered before the buck, or if the order in which he was exposed to the two does changed on different days.

Mating behavior

The buck was introduced to the 1½-year-old doe at 3:00 PM on 16 November 1965. She stood in a stationary position and he immediately attempted to mount her. He attempted to copulate with her 12 times and terminated the twelfth mount with a heavy thrust, pushing her forward and immediately dismounting. He then rubbed her back with his muzzle and made no further attempts to mount her in the 30 minutes that they remained together.

At 5:00 PM on 16 November 1965, the 2½-year-old doe was introduced to the buck. She stood in a stationary position, and after a few attempts at mounting, he copulated with her and gave a terminal thrust. He made no further attempts to mount her in the remaining 30 minutes.

At 9:00 PM on 16 November 1965, the buck was again placed in the breeding pen with each doe, but he made no attempts to mate with either of them.

Behavior during the days after mating

In order to allow for a successful mating if the does had not conceived on 16 November, they were exposed to the buck using the same procedure outlined previously, until at least two more estrus cycles would have occurred, assuming a cycle length of 12-14 days. No further matings occurred, although on 4 December 1965, the buck twice attempted to mount the 1½-year-old doe but she walked away from him on each occasion and he did not make further attempts.

Behavior of the deer when not in the breeding pen

The 1½-year-old doe was not easily approachable, but on 16 November 1965, when in estrus, she was unusually inactive. The 2½-year-old doe could normally be touched on the head but

not closely approached in her pen. When in estrus, she was very docile and could be thoroughly examined. Prior to 16 November 1965, she often had to be forced to enter the breeding pen. When in estrus she entered readily, but after that time she could not even be forced to enter the pen on several occasions. The buck could usually be approached and handled but was often very aggressive towards the investigator.

Fetuses

The 1½-year-old doe was sacrificed on 18 January 1966 and twin male fetuses were obtained. A male and a female fetus were obtained from the 2½-year-old doe when she was sacrificed on 28 February 1966. Morphological descriptions and measurements of these animals are given in other sections.

2. EVALUATION OF EXTERNAL DIMENSIONS

Some measurements taken on the fetuses are of more value than others. The value of the measurements is determined by their repeatability, and if accurate, by their usefulness in studying growth.

The degree of accuracy is governed by several factors. One factor is the shape in which an animal was preserved.

Many fetuses were preserved in unnatural positions and portions of their bodies were fixed in stretched or twisted positions. Even if all animals were held in a similar manner when being examined, the position in which they were fixed may have some influence on the accuracy of the measurements. Circumferential measurements may in some cases be less affected than linear measurements. The distortion of a circumference in one plane may compensate for distortion in another plane.

Another factor that may influence accuracy is the points of reference used to evaluate the dimension. When the measurement is taken between two surface structures, the point of reference may be located with great accuracy. If the measurement is taken using skeletal structures (by palpitation), it may be more difficult to locate the points of reference, depending on how much soft tissue covers them. No specific structure could be consistently designated as the lambdoidal crest and in most animals the tail head was difficult to locate. Measurements based on these structures are therefore of limited value and were seldom taken. These include the total spine length, precaudal spine length, withers to tail head and dorsal tail length. The greater trochanter of the femur is often greatly obscured by soft tissues. Consequently the length of the femur and bitrochanteric diameter were often difficult to assess.

Many circumferential measurements are difficult to take with accuracy due to the subjective problem of passing the measuring thread along the same pathway on each occasion.

Although many measurements may be repeated with little deviation on the same animal, they may not be comparable to those of other specimens due to individual variation in the amount of subcutaneous tissue and muscle covering bones, and differences in stretching and twisting of form. Indeed, valid comparison may not be possible between different dimensions of the same animal due to distorted morphology resulting from preservation.

During the growth of the fetus, certain morphological changes are of such magnitude that comparable measurements can be taken in the same structural areas for only a portion of the fetal period. In this category are crown-rump length, head width and vertical head circumference. Certain measurements taken on animals lacking hair are not comparable to those taken on animals with hair, due to the increase in surface thickness.

Obviously, structural damage can cause inaccuracies in mensuration and must be guarded against. The soft non-keratinized terminal portions of the hoofs are easily broken. Measurements involving the hoof points were made before taking other measurements.

It should be noted that although the dimensions of certain small structures may be measured with great accuracy, the change during growth may be negligible compared to large dimensions that cannot be measured with equal precision.

3. EFFECTS OF PRESERVATION ON RESULTS

Numerous workers (such as Patten and Philpott, 1921) have studied the changes that may occur in tissue after preservation in various fluids. Weights and dimensions of fetuses may change after preservation, and consideration must be given to such changes when reviewing quantitative data. The following examples illustrate the changes that occurred after preservation of fetal material in formol saline. These data probably reflect changes induced by preservative fluid, human error in measuring, and changes induced by fixation in a twisted or stretched position.

Changes in weight

Five in a group of six animals that were weighed when fresh and then weighed again after remaining in formol saline for two months experienced a mean weight loss of 6.59%. One fetus gained 3.19%. The range of loss was from 2.11% to 14.44%.

Sixteen animals were weighed when fresh and weighed again after two years in formol saline. All lost weight, with a mean loss of 10.86% and a range of 1.97% to 15.87%.

There appears to be no relationship between forehead-rump length and amount of weight change or between fresh weight per unit length and amount of weight loss. However, these data suggest that the length of time a fetus is preserved should be considered when evaluating the situation in the fresh animal.

Changes in linear and circumferential dimensions

Table I illustrates the changes in 27 measurements after formol saline preservation. These changes were evaluated using a t-test.

TABLE I

MEASUREMENTS OF A SERIES OF FETUSES
BEFORE AND AFTER PRESERVATION IN FORMOL SALINE

MEASUREMENT	FETUS #	BEFORE	AFTER	SIGNIFICANCE OF CHANGE
Forehead-rump length	1	78.4mm	74.5mm	*
	2	81.2	76.2	
	3	205.0	192.5	*
	4	204.0	187.5	
Head length	1	28.6	25.5	ns.
	2	27.0	25.9	
	3	68.3	68.0	ns.
	4	66.5	67.8	
Face height	3	28.7	32.5	*
	4	26.8	31.9	
Diameter at nares	1	5.3	5.6	ns.
	2	5.2	6.0	
	3	15.4	15.9	*
	4	15.3	16.0	
Interorbital breadth	1	10.9	12.0	ns.
	2	10.9	13.2	
	3	31.8	31.0	ns.
	4	31.0	31.2	
Diameter of orbit	1	5.2	5.7	ns.
	2	4.5	4.5	
	3	11.9	11.2	ns.
	4	11.4	11.4	
Bizygomatic breadth	1	16.7	15.3	ns.
	2	15.4	15.7	
	3	34.8	35.5	ns.
	4	33.8	35.2	

NOTE: Fetuses numbered one and two were preserved for four months before being remeasured. Fetuses numbered three and four were preserved for two and one half months.
 ns. = not significant.
 * = $0.01 < P < 0.05$.
 ** = $P < 0.01$.

TABLE I (continued)

MEASUREMENT	FETUS #	BEFORE	AFTER	SIGNIFICANCE OF CHANGE
Ear length	3	24.1mm	24.3mm	ns.
	4	24.0	25.5	
Preoptic length	1	12.2	11.4	ns.
	2	11.5	11.6	
	3	33.3	32.9	ns.
	4	31.4	31.4	
Postoptic length	1	10.4	9.9	ns.
	2	10.9	9.7	
	3	31.9	30.5	ns.
	4	30.8	31.0	
Shoulder to pin	1	45.4	39.1	ns.
	2	43.4	41.1	
Shoulder to hip	1	33.3	30.6	*
	2	33.6	31.5	
Neck length	3	55.0	40.6	**
	4	52.8	40.5	
Transverse chest diameter	3	34.0	38.0	ns.
	4	35.4	37.4	ns.
Sagittal chest diameter	3	49.5	49.5	ns.
	4	48.8	50.7	
Ventral tail length	1	6.7	5.9	ns.
	2	7.2	5.6	
Hip width	3	26.0	22.8	ns.
	4	26.0	25.2	
Biochanteric diameter	3	30.9	30.6	ns.
	4	32.2	33.3	
Length of humerus	3	38.2	38.6	ns.
	4	38.4	38.2	

TABLE I (continued)

MEASUREMENT	FETUS #	BEFORE	AFTER	SIGNIFICANCE OF CHANGE
Length of foreleg	1	28.8mm	27.0mm	ns.
	2	27.4	26.7	
	3	93.2	89.8	*
	4	92.4	87.9	
Length of forefoot	3	50.5	50.6	ns.
	4	49.7	49.5	
Length of femur	3	43.5	37.3	ns.
	4	38.0	39.7	
Length of hind leg	3	97.9	98.8	ns.
	4	99.9	97.0	
Length of hind foot	3	73.8	71.2	ns.
	4	72.2	71.4	
Median neck circumference	3	82.5	82.5	ns.
	4	71.0	75.0	
Chest circumference	3	136.5	141.0	ns.
	4	141.0	141.0	
Abdominal circumference	3	146.0	143.0	ns.
	4	139.0	144.0	

B. GENERAL DESCRIPTION

The general morphology of the fetus and the basic patterns of development are discussed in this section.

1. VIBRISSAE AND PIGMENT PATTERNS

The appearance of vibrissae, hair patterns and colouration of the skin (in many regions resulting from the underlying hair follicles) provide useful landmarks in the study of the development of the fetus. Some special regions of vibrissae and pigmentation that may be observed as the fetus grows are described here.

VIBRISSAE FOLLICLES AND VIBRISSAE

Vibrissae follicles appear as small white spots or elevations, from which emerge vibrissae in the following regions:

Mystacial vibrissae occur on the dorsal and lateral anterior sides of the skin of the rostrum and upper lip.

Submental vibrissae are found on the anterior, lateral and ventral surfaces of the skin covering the anterior end of the lower jaw.

Interramal vibrissae are found on the skin between the rami of the lower jaw.

Malar vibrissae are found on the skin of the ventral half of the lateral side of the head.

Superciliary vibrissae are located directly above the upper eyelid and extend anterior to the eye.

Ciliary vibrissae form lines along the edges of the eyelids.

Subciliary vibrissae are found on the skin of the head immediately below the lower eyelid and extend anterior to the eye.

Never more than three interramal vibrissae have been found and never more than one pair of malar vibrissae have been found on each side. The vibrissae of other regions are numerous. As the vibrissae increase in number and length as the animal grows, they may be used as one criterion for determining the level of development of the fetus.

PIGMENTATION

Inferior nasal pigment is present on the anterior surface of the upper lip and ventral anterior nose.

Superior nasal pigment extends between the external nares from the dorsal surface of the nose anterior to the posterior borders of the nares to the dorsal border of the inferior nasal pigment.

The superior labial line is a line of pigment that extends along the upper lip.

The inferior labial line is a line of pigment that extends along the lower lip.

The ciliary line is a line of pigment that appears at the site of emergence of the ciliary vibrissae.

The presence or absence, colour and intensity of pigment in any region may be used as an indication of the level of development of the fetus.

2. OUTLINE OF EXTERNAL DEVELOPMENT

An understanding of the general pattern of fetal development for the organism as a whole may be gained by studying a series of stages of development. Witschi (1956), for example, lists a series of periods and standard stages of development for vertebrates. A table of "normal stages" is of obvious importance to experimental work. The stages described here are based mainly on readily discernible morphological features, not size or age (ages are listed for only two stages). Balinsky (1960) points out that size and age are, in general, poor criteria for indicating the extent of

development. He favors the use of external morphological properties for defining stages.

The stages included in this outline of development are based only on the material available for examination. Stage I, therefore, represents the smallest fetus available. A more finely refined series of stages will probably be possible, when more specimens are collected. The description of each stage of development is based on what is considered to be a representative animal. These animals were chosen to illustrate the state of development of the fetus at a series of instants during growth and thus demonstrate the relationship between different morphological changes as growth progresses. The animals selected are spaced so as to minimize the effects of individual variation obscuring the general pattern. The structure of sex-specific characters is included for both sexes by referral to specimens considered to be of comparable levels of development although of the opposite sex to the chosen typical specimens. The measurements, however, are those of the chosen typical specimen.

Hair colour as described is in reference to the general appearance of the pelage, rather than the individual hairs, many of which contain several colour bands. General

surface hair colour may thus change in a given area as new bands emerge during development, even though the same hairs are present.

STAGE I. Crown-rump length, 24.2 mm., bizygomatic breadth, 8.3 mm., weight, 1.5 grams.

1. In general form, the animal is flexed so that it resembles the letter "C." The muzzle is directed ventrally and caudally and lies in apposition with the ventral aspect of the thorax and between the front hoofs. Flexures apparent are the cephalic, pontine, cervical, dorsal, and lumbo-sacral.
2. Regions of the brain evident externally are the telencephalon, mesencephalon and myelencephalon. The mesencephalon forms a conspicuous prominence.
3. The eyes are very distinct. No eyelids are present and no preorbital fold is evident.
4. The auricles of the ears are present as small folds that are directed ventrally. The external auditory meatuses are closed, but not completely covered by the auricles.
5. The nares are distinct but closed.

6. The mouth is open and the tongue protrudes.
7. The neural arches of the vertebrae are not complete and the spinal cord is distinguishable for its total length.
8. The liver prominence is very conspicuous.
9. The phallus is large and curved caudad.
10. The hoofs and dew claws are differentiated. The hind foot is less than twice the length of the tail.
11. No hair or pigment is evident on the animal.
12. Vibrissae follicles are present in the mystacial, submental, interramal, malar, subciliary and superciliary areas.

STAGE II. Forehead-rump length, 45.2 mm., bizygomatic breadth, 9.5 mm., calcaneus-hoof length, 9.2 mm., weight, 4.34 grams.

1. In general form, the animal is not curled, most of the dorsal surface lying along the same plane. The muzzle is directed ventrally and lies anterior to the thorax and front hoofs. The region of the pontine flexure is not distinct.
2. The region of the cerebral hemispheres is evident and the mesencephalon forms a conspicuous prominence.

3. The eyelids are partially formed but the eyes are open. A distinct preorbital line is present. Pigment is visible in the region of the iris.
4. The auricles of the ears are folded in a ventral direction and completely cover the external auditory meatuses. The meatuses are closed.
5. The nares are closed.
6. The sides of the mouth are closed by membranes, but the front of the mouth is open. The tongue does not protrude from the mouth.
7. The neural arches of the vertebrae are not complete and the spinal cord may be distinguished externally for its entire length. The cord is partially enclosed for much of its length, most noticeably in the thoracic region.
8. The abdomen is more ventrally extended than the thorax. The area of the liver is distinct externally.
9. The phallus is curved caudad. Two distinct genital swellings are evident, one on each side of, but slightly posterior to the phallus in the male, but more anterior in the female.

10. One pair of teats is situated lateral to the phallus on each side.
11. No hair or pigment is evident on the animal.
12. Vibrissae follicles are present in the mystacial, submental, interramal, malar, subciliary and superciliary areas.

STAGE III. Forehead-rump length, 74.5 mm., bizygomatic breadth, 25.5 mm., calcaneus-hoof length, 17.7 mm., weight, 14.5 grams. Age, 63 days.

1. The general body form and proportions resemble those of an adult. The body axis is somewhat curved.
2. In general form, the head is elongate. The frontal region is quite high however, and forms a steep angle to the mouth. The muzzle is a prominent feature of the head. The cerebral hemispheres are distinct. The frontals and parietals are evident as lateral plates.
3. The regions of the eyes protrude noticeably. The eyelids are formed and the eyes are closed. The pigment of the iris is visible. A preorbital fold is distinct.

4. The auricles of the ears are partially unfolded from the sides of the head but are directed ventrally and laterally. The external auditory meatuses are closed.
5. The nares are closed.
6. The mouth is completely closed. The lips are distinct. The lower lip extends more anterior than the upper lip. Lateral membranes are present between the lips.
7. The spinal cord is almost completely enclosed by the neural arches of the vertebrae.
8. The area of the liver is distinct externally but the ventral plane of the abdomen is confluent with that of the thorax.
9. The penis is mainly straight in form and is directed ventrally. The scrotum is evident as two distinct but medially united swellings posterior to the penis. The clitoris is prominent and directed posterior and dorsally. It has begun to take on its adult form.
10. The limbs are conspicuous, slender and long. The hind foot is greater than twice the length of the tail.

11. No hair or pigment is evident on the animal.
12. Vibrissae follicles are present in the mystacial, submental, interramal, malar, subciliary, and superciliary areas.
13. Two teats are present on each side of the ventral posterior abdomen.

STAGE IV. Forehead-rump length, 103.2 mm., bizygomatic breadth, 20.8 mm., calcaneus-hoof length, 27.3 mm., weight, 42.88 grams.

1. The cerebral hemispheres are prominent. The frontal region forms an abrupt angle between the crown and the mouth.
2. The frontals and parietals are distinct on the dorsal aspect of the head but the dorsal borders of each side are separated by a distinct gap.
3. The pigment of the iris is visible.
4. The auricles of the ears are directed dorsally and medially and the external auditory meatuses are closed. The distance between the distal tips of the auricles when folded back flat against the head is less than the length of one auricle.
5. The nares are closed.

6. The mouth is closed and the lips are very well developed. The lower lip is large and extends noticeably more anterior to the upper.
7. The submental region of the lower jaw is poorly developed, giving the anterior end of the snout a pointed appearance when viewed from the side.
8. The penis is straight and directed anteriorly. The scrotum is in the form of a small bilobed structure posterior to the penis.
9. Antler primordia are present on the dorso-lateral aspects of the head in both sexes.
10. Metatarsal glands are present on the lateral sides of the hind feet.
11. No hair or pigment is evident on the animal.

STAGE V. Forehead-rump length, 187.5 mm., bizygomatic breadth, 35.2 mm., calcaneus-hoof length, 66.5 mm., weight, 259 grams. Age, 103 days.

1. The head is elongate, the rostrum is prominent, and the frontal region does not form a steep angle to the mouth.
2. The frontals and parietals are palpable over most of the dorsal region of the head but a small

but distinct space separates most of the length of their dorsal borders.

3. The closed eyes form large protuberances on the sides of the head. The pigment of the iris is visible through the eyelids.
4. The auricles of the ears are directed medially against the head and the distal edges of the auricles overlap each other for a distance greater than one half the length of one auricle. When folded medially, the distal border of one auricle does not reach the external auditory meatus of the opposite side. The external auditory meatuses are closed.
5. The nares are closed.
6. The mouth is closed. The submental region of the lower jaw is well developed, giving the anterior end of the muzzle a blunt appearance when viewed from the side. The periodontal ridge is distinct. The positions of the incisors and canines are not apparent. The insides of the lower lips are distinctly serrated. Horizontal ridges on the tongue are poorly defined.

7. The penis is directed anteriorly and the scrotum is of a pendulous nature. The clitoris is large and is directed posteriorly. It is the prominent feature of the genital region, obscuring much of the labia.
8. The hind foot is greater than three times as long as the tail.
9. Several areas of pigmentation are evident on the skin. The superior nasal pigment is present, mid-brown in colour, with white spots. The inferior nasal pigment is evident as light brown with white spots. The light brown superior and inferior labial lines are difficult to distinguish. A light brown ciliary line is present. The anterior proximal regions of the hoofs are faintly pigmented.
10. Some vibrissae are present on the head. Subciliary and superciliary vibrissae are just beginning to emerge. Very short malar and interramal vibrissae are present. A few mystacial and submental vibrissae are evident.

STAGE VI. Forehead-rump length, 226.5 mm., bizygomatic breadth, 40.7 mm., calcaneus-hoof length, 89.5 mm., weight, 436.80 grams.

1. The dorsal borders of the parietals are in close proximity. The frontals appear to be in apposition anteriorly. A distinct anterior fontanelle is present.
2. The pigment of the iris is not readily visible through the closed eyelids.
3. The auricles of the ears are directed medially and folded onto the dorsal aspect of the head. The distal border of one auricle reaches to the external auditory meatus of the other side of the head. The external auditory meatuses are slightly opened.
4. The nares are somewhat opened.
5. The periodontal ridge is distinct. The positions of individual incisors and canines can be detected at different regions of the ridge. The insides of the lips are distinctly serrated.
6. The scrotum is pendulous and distinctly longer than the penis. The clitoris occupies a smaller portion of the genitalia, the labia being clearly visible.
7. The superior nasal pigmentation is dark brown with white spots. The inferior nasal pigmentation

is light brown with white spots. The inferior labial line is mid-brown and the superior labial line is light brown. The proximal portions of the hoofs are pigmented. Some dorsal white spots are evident on the skin of the trunk.

8. Vibrissae are present in the mystacial, submental, interramal, malar, superciliary, ciliary, and subciliary areas.
9. Hairs are detectable on the skin covering the olecranon region, the posterior distal region of the femur, the ventral thoracic region, the ventral abdomen anterior to the umbilical cord, and the ventral and lateral neck.

STAGE VII. Forehead-rump length, 269.5 mm., bizygomatic breadth, 46.0 mm., calcaneus-hoof length, 108.5 mm., weight, 730 grams.

1. Most of the skin is very light brown in colour, but the rump, ventral abdomen, much of the medial surfaces of the limbs and the ventral side of the head and tail are white. On close examination hair may be seen emerging over much of the body surface.

2. The anterior fontanelle is distinct.
3. The pigment of the iris is not visible through the closed eyelids.
4. The auricles of the ears are directed medially and folded onto the dorsal aspect of the head. The distal border of one auricle can completely cover the external auditory meatus of the opposite side. The external auditory meatuses are noticeably open. When folded forward, the distal tips of the auricles reach just to the posterior borders of the eyes.
5. The mouth is closed. The tooth ridge and positions of the developing incisors and canines are very distinct. The horizontal ridges on the tongue are well defined.
6. The superior nasal pigmentation is dark brown with white spots. The inferior nasal pigmentation is light brown with white spots. The ciliary line is very distinct. The skin of the dorsal surfaces of the auricles of the ears is brown with white margins. The proximal portions of the hoofs are distinctly pigmented. Both dorsal and lateral white spots are apparent on the skin of the trunk.

7. Hair on the body surface is sparse, but most readily evident on the skin covering the olecranon region, the lateral distal region of the humerus, lateral proximal region of the ulna, the posterior lateral region of the femur, lateral region of the tibia, the lateral borders of the ventral surface of the thorax, a thin mid-ventral line between the thorax and umbilical cord and the regions of the antler primordia of the head. Dark-coloured hairs are beginning to emerge over much of the body surface.
8. White hairs are apparent on the skin covering the medial surfaces of the legs in the regions of the humerus and radius, and on the regions of the femur and tibia, on the posterior ventral regions of the abdomen, on the ventral surfaces of the auricles of the ears and on the ventral side of the head.
9. Areas of the crown, rostrum, feet and tail show no evidence of emerging hair.

STAGE VIII. Forehead-rump length, 284.0 mm., bizygomatic breadth, 52.0 mm., calcaneus-hoof length, 123.4 mm., weight, 850 grams.

1. In general appearance, the animal is light grey with some white areas. Hair is generally sparse but varies in density in different areas.
2. The mouth is closed. The inferior labial line is mid-brown and the superior labial line is light brown. The ridges on the roof of the mouth are mid-brown in colour. The inferior nasal pigmentation is mid-brown with white spots and the superior nasal pigmentation is dark brown with white spots.
3. The proximal borders of the hoofs are dark brown.
4. Faint white spots are present on the skin of the dorsal and lateral surfaces of the trunk. White spots are present on the lateral sides of the legs in the region of the humerus and the femur.
5. The remainder of the animal is light grey except for the following white areas: the ventral surface of the tail, abdomen, medial surfaces of the hind legs down to the level of the hock joint, medial surfaces of the pectoral limbs down to the level of the distal end of the radius, a ventral

surface of the head except for a grey chin band, ventral surfaces of the auricles (except for a posterior portion, peripheral bands on the dorsal surfaces of the auricles, distal regions of the hoofs, dew claws, the central region of the metatarsal glands.

6. The animal is sparsely haired over much of its body surface. In general, dark-coloured hairs are present on areas of dark pigment and white-coloured hairs are present on the white areas.
7. The hair on the skin covering the olecranon region has a golden brown appearance, as does that of the antler primordia and supraorbital regions.
8. The hair of the crown is short but dense and completely obscures the underlying skin. A dark brown face-band is beginning to appear. A throat-band of brown hair is evident.
9. Except for specific areas, very little hair is present on the feet. Bands of golden brown bristles border the proximal edges of the hoofs. A distinct ring of hair borders the area of the tarsal gland. The anterior border is gold and the posterior border is brown. Except for the

areas mentioned, hair is difficult to locate distal to the calcaneus of the hind foot. Hair is beginning to emerge on the front feet where hair is not present on the hind feet.

10. No white hairs are evident emerging from the white spots on the trunk.
11. Lateral anterior regions of the rostrum are free of hair.

STAGE IX. Forehead-rump length, 328.5 mm., bizygomatic breadth, 56.9 mm., calcaneus-hoof length, 142.5 mm., weight, 1260 grams.

1. In general appearance, hair may be seen on the skin over most of the body surface. The hair is generally short and not dense enough to obscure the skin in most areas. Most of the body appears dark grey or white.
2. The mouth is closed. The ridges on the roof of the mouth have areas of mid-brown pigmentation. The inferior nasal pigmentation is mid-brown with white spots, and the superior nasal pigmentation is dark brown in colour.
3. The proximal regions of the hoofs are dark brown.

4. The hair of the crown gives it a golden brown appearance. Black hairs are present at the location of the antler primordia and an area of black hair is beginning to appear on the front of the face. The skin bordering the eyelids lacks hair and the skin around the lateral sides of the anterior end of the muzzle lacks hair (other than mystacial vibrissae). The skin covering the lateral sides of the head ventral to the eyes is covered by light brown hair. A submental band of black hair breaks the white ventral surface of the head. Skin is visible at the site of emergence of the superciliary vibrissae. Pigmented skin is visible on the borders of the dorsal surfaces of the auricles of the ears. Hairs surrounding the external auditory meatuses are obvious.
5. Long hair along the border of the dark trunk and white rump gives this area a light brown appearance. White hairs on the ventral surface of the tail are several mm. long. Virtually no hair is visible on the white rump. Small white ends of hairs just beginning to emerge are visible. White hairs are present on the white trunk spots.

6. Hair is distinct on the tarsal glands. Each gland is surrounded by a peripheral light brown band of hair.
7. Hair is evident on the feet. It is easily seen on the hind feet as far distally as the metatarsal gland. The metatarsal gland is lined by a thin border of dark brown hair and an inner brown band of hair surrounding the central gland area.

STAGE X. Forehead-rump length, 330.5 mm., bizygomatic breadth, 49.8 mm., clacaneus-hoof length, 140 mm., weight, 1,002 grams.

1. In general appearance, the animal is covered with a short but dense coat of hair, giving a velvety appearance to the body surface.
2. The superior nasal pigmentation is dark brown with white spots. The inferior nasal pigmentation is mid-brown with white spots. The superior and inferior nasal lines are mid-brown. Grey areas are apparent on the roof of the mouth. The positions of the incisors and canines are distinct under the periodontal membrane.
3. Most of the head is covered in hair that gives a golden brown appearance. Grey-appearing skin is

visible on the anterior lateral regions of the rostrum. A black strip of hair is present from the posterior margin of the superior nasal pigmentation to the frontal region where it extends laterally on each side to end in a black band over each eye. Black patches of hair are present at the sites of the antler primordia. A strip of white hair is present along the lateral margin of each upper lip. The ventral surface of the head is covered with white hair except for a submental band of hair - golden brown with two black lateral anterior extensions and one brown and black mid-ventral anterior extension. The vibrissae of the head are clearly distinguishable as they are of much greater length than the hair of the head.

4. The dorsal surfaces of the auricles of the ears are covered with hair forming black and dark brown regions. A region of white hair is present at the posterior proximal edge of each auricle. Peripheral margins of brown pigmented skin are visible on the auricles. The ventral surfaces of the auricles are sparsely covered with brown pigmented skin that is clearly visible.

5. The dorsal and lateral surfaces of the trunk have a dark brown dense velvet covering of hair with spots of white hair extending down to the skin covering the humerus and femur.
6. The colour of the dorsal surface of the tail is dark brown and continuous with the dark brown of the trunk.
7. The medial surfaces of the legs down to the feet, the ventral surface of the abdomen and the ventral surface of the tail are sparsely covered in white hair. The genital organs are covered in white hair.
8. The ventral thorax and ventral and lateral neck are light brown in colour.
9. The feet are covered in short but dense hair giving them a dark brown appearance. The front feet are a lighter brown colour than the hind feet. Long hairs giving a gold appearance cover the proximal borders of the hoofs.
10. The metatarsal glands are surrounded by a border of long gold-coloured hairs. The skin of the central glandular area is visible.

11. The tarsal glands are bordered by long white hairs but the central depression of the gland is not obscured by these hairs.

STAGE XI. Forehead-rump length, 334 mm., bizygomatic breadth, 56.9 mm., calcaneus-hoof length, 159.0 mm., weight, 1,345 grams.

1. In general appearance, most regions of the body are well covered with hair.
2. Grey pigmented skin is visible posterior to the nares and lateral and ventral to the posterior ends of the nares.
3. The superior nasal pigmentation is black and the inferior nasal pigmentation is dark brown.
4. The crown is golden brown in colour and the black band of hair covering the dorsal surface of the rostrum and branching over the eyes is very distinct. Black areas of hair are present over the antler primordia.
5. The dorsal surfaces of the auricles of the ears are covered with hair that gives a dark brown appearance, with some golden brown in the central areas. White hair is present on the skin of the

posterior proximal borders of the auricles. A peripheral band of brown pigmented skin is visible at the distal edges. The brown pigmented skin of the distal surfaces of the auricles is sparsely covered with white hair. White hair is present on the anterior fold of skin that is continuous with the skin of the dorsal surfaces.

6. The non-white hairs covering the dorsal surface of the trunk give it a dark to golden brown colour. The hair of the distal end of the dorsal surface of the tail is black, whereas the hair on the proximal end of the dorsal surface of the tail appears dark brown.
7. The trunk is covered with white spots that extend from the dorso-lateral surfaces to the skin covering the femur and humerus. The white hairs of the trunk spots are long enough that some of the spots appear confluent.
8. The ventral surface of the abdomen is covered with hair that is quite long but not dense in the posterior regions. The genital organs are not obscured by hair and the teats are distinct.

9. The medial surfaces of the legs down to the level of the feet are covered with white hair that is long and relatively dense.
10. The hair of the feet gives them a mid-brown to golden brown appearance. Gold-coloured rows of hair border the proximal surfaces of the hoofs. A gold band of hair lines each metatarsal gland, almost obscuring the central region. The keratin of the hoofs is pigmented dark brown over most of the dorsal surfaces and much of the way down the lateral surfaces.
11. The tarsal gland is bordered by a thick white mass of hair, but the central area is not obscured completely.

STAGE XII. Forehead-rump length, 448 mm., bizygomatic breadth, 63.5 mm., calcaneus-hoof length, 232.5 mm., weight, 2,834 grams.

1. In general appearance, the animal has a thick, dense covering of long hair.
2. The skin on the lateral anterior regions of the rostrum and the borders of the external nares is covered with black hair.

3. The superior nasal pigmentation is black. The inferior nasal pigmentation is black with white spots.
4. The incisors and canines have erupted.
5. Patches of dark grey pigmentation are present on the roof of the mouth.
6. The hair of the head is mostly golden brown and light brown in appearance except for the black dorsal rostral band, supraorbital bands, antler primordia and lateral anterior rostral areas. The ventral surface of the head is white except for the brown and black chin band. Bands of white hair border the lateral sides of the upper lips. The hair bordering the eyes and ventral surface of the preorbital glands is very light in colour.
7. Most of the dorsal surfaces of the auricles of the ears are covered with golden brown hair. No distal region of peripheral pigmented skin is visible. Some white hair is visible at the tip of the auricles and on the proximal anterior and posterior borders. Much long white hair is present on the ventral surfaces of the auricles, but pigmented skin is visible there also.

8. The trunk is covered with golden brown and light brown hair with white spots. The whitespots do not have well-defined borders. The pelage is of such length that the spots appear more as tufts of white hair.
9. The hair of the tail has a very thick woolly appearance.
10. The hair of the legs is light brown in appearance and the metatarsal glands are completely obscured by long hair of a light brown colour.
11. The tarsal gland is obscured by hair and the general gland area has a thick woolly appearance.
12. The hoofs are almost completely enclosed in keratin, which is pigmented dark brown except for the distal borders.
13. The medial surfaces of the legs as far down as the feet are covered in white hair. The ventral side of the tail is covered in white hair. The abdomen and rump are covered in dense white hair and the genital organs of the male are difficult to locate due to the thickness of the hair covering.

3. PATTERNS OF GROWTH

The size relationships during growth of various body dimensions are represented by the following data. As proportions during growth tend to be a function of absolute size rather than absolute age (Reeve and Huxley, 1945), patterns of relative growth may be described without reference to time.

The relationship of growing parts is represented here by the allometric equation $Y = b X^k$, where Y and X are the dimensions being studied, k is the growth ratio at which Y grows in relation to X, and b is a constant specific to the dimensions being considered. It is the value of Y when X^k is unity (or the ratio of Y to X when $k = 1$). The value of b is not biologically significant. The allometric equation is used to represent the relationship in each pattern of growth described. In each case, an IBM 7040 computer made a standard least squares straight line fit to the transformed equation $\log_{10} Y = \log_{10} b + k \log_{10} X$. The program was written in FORTRAN IV.

In addition to studying specific regional growth relationships, all dimensions considered have been related to both forehead-rump length and calcaneus-hoof length. The former provides a basis of comparison to total body length; a common basis to which all data may be compared. It also facilitates

comparison of these data to those of other investigators. Calcaneus-hoof length, however, is probably a more accurate and precise measurement and appears to correlate better with differentiation rates. It has therefore been presented as an alternative method of expressing growth.

Table II represents a comparison of the equations for the growth of structures relative to forehead-rump length. Similarly, in Table III may be seen growth relative to calcaneus-hoof length.

It should be emphasized that all the "growth patterns" described in this section have been synthesized after determining the relative dimensions of a series of distinct fetuses, rather than obtaining data continuously from the same individuals.

Figures 1 - 44 (which appear in the Appendix) are graphic representations of relative growth. Each observation is represented by a + (plus) sign. The centroid is represented by an $\bar{x}$. Two x symbols represent actual points on the line fitted to the data.

In examining the data for general trends, the tables and graphs are in most cases self-explanatory. They illustrate the growth patterns of the fetus and thus provide basic information for future investigators. The tables are constructed in order of slope, from highest to lowest k values. All the lines fit the data below the 5% level of significance and many are significant fits below the 1% level. The following comments will aid in

interpreting the more critical relationships in the data. All the patterns to be discussed have been evaluated using t-tests. In the case of multiple comparisons, the significance levels cannot be compared with validity, but are useful as general indicators.

Growth of the head

In relation to forehead-rump length and calcaneus-hoof length, the cranium appears to grow in diameter more rapidly than the interorbital region ($.01 < P < .05$). In length however, the cranium does not grow significantly faster than the rostrum. This is in marked distinction from post-natal growth during the early phases of which the rostrum gains more rapidly than any other skull area.

Growth of the trunk

Compared to forehead-rump length, the neck appears to grow relatively faster in circumference than the abdomen ($.01 < P < .05$). When calcaneus-hoof length is used as a basis of comparison, the chest appears to grow relatively faster in circumference than the neck ($.01 < P < .05$) which grows faster than the abdomen ($P < .01$). In any comparison, there is no evidence that the pelvic region grows significantly faster in width than

does the thorax. When comparing the length of the innominate bone to the distance between the crests of the ilia, it appears that the pelvis grows relatively faster in length than in width ($P < .01$).

Growth of the limbs

Each of the components of the hind limbs appear to grow relatively faster than the corresponding components of the fore limbs ($P < .01$). Thus the femur grows relatively faster than the humerus and the tibio-fibula and hind foot grow relatively faster than the ulna and forefoot.

Relative growth in general

From examining Table II and Table III, it can be seen that the k values maintain essentially the same sequence. The rates of growth of the transverse chest diameter and bizygomatic breadth differ in position in the two tables. The ears grow (in length) relatively faster than any other structure. Indeed, using forehead-rump length as a basis of comparison, the ears grow faster than the calcaneus-hoof length ($P < .01$). The calcaneus-hoof length increases more rapidly than the total length of the hind leg ($P < .01$).

Equations have been derived from the data of Armstrong (1950), who studied fetal development in the Northern white-tailed deer, and Hudson (1956), who studied the fetal development of the Rocky Mountain mule deer. These equations are compared to the patterns of growth of the Columbian black-tailed deer fetus in Table IV.

TABLE II

PATTERNS OF GROWTH IN THE FETAL PERIOD OF THE RELATIONSHIP

 $Y = b X^k$ WHERE X REPRESENTS FOREHEAD-RUMP LENGTH

Y	b	k
Weight	.0001315	2.756
Ear length	.002455	1.740
Calcaneus-hoof length	.03917	1.422
Length of hind leg	.0588	1.413
Length of foreleg	.09268	1.313
Length of femur	.05047	1.271
Length of humerus	.06839	1.213
Hip bone to pin bone	.07745	1.174
Ventral tail length	.07129	1.110
Chest circumference	.8921	.9639
Cranial length	.2417	.9619
Preoptic length	.2011	.9519
Median neck circumference	.6024	.9254
Abdomen circumference	1.432	.8719
Hip width	.2463	.8699
Transverse chest diameter	.3992	.8408
Bizygomatic breadth	.4608	.8179
Interorbital breadth	.4506	.7763

TABLE III

PATTERNS OF GROWTH IN THE FETAL PERIOD OF THE RELATIONSHIP

 $Y = b X^k$ WHERE X REPRESENTS CALCANEUS-HOOF LENGTH

Y	b	k
Weight	.04764	2.020
Ear length	.1292	1.2223
Length of hind leg	1.479	.9917
Length of foreleg	1.852	.9224
Length of femur	.9177	.8916
Length of humerus	1.080	.8538
Hip bone to pin bone	1.119	.8249
Ventral tail length	.7713	.8129
Chest circumference	8.050	.6757
Cranial length	2.183	.6742
Preoptic length	1.749	.6708
Median neck circumference	4.925	.6514
Abdomen circumference	10.424	.6137
Hip width	1.790	.6111
Bizygomatic breadth	2.734	.5938
Transverse chest diameter	.2726	.5891
Interorbital breadth	2.579	.5504

TABLE IV

COMPARISON OF FETAL GROWTH PATTERNS IN THREE FORMS OF DEER

 $Y = b X^k$ WHERE X REPRESENTS FOREHEAD-RUMP LENGTH

Y	<u>Odocoileus</u> <u>hemionus</u> <u>columbianus</u>	<u>Odocoileus</u> <u>hemionus</u> <u>hemionus</u>	<u>Odocoileus</u> <u>virginianus</u> <u>borealis</u>
Length of hind leg	$Y = .0588X^{1.413}$	$Y = .06637X^{1.405}$	$Y = .09797X^{1.299}$
Length of foreleg	$Y = .09268X^{1.313}$	$Y = .09770X^{1.316}$	$Y = .09745X^{1.292}$
Chest circumference	$Y = .8921X^{.9639}$	$Y = .8754X^{.9716}$	$Y = .7017X^{.9908}$
Median neck circumference	$Y = .6024X^{.9254}$	$Y = .4132X^{.9528}$	$Y = .3134X^{1.029}$
Abdomen circumference	$Y = 1.432X^{.8719}$	$Y = 1.592X^{.8555}$	$Y = .8654X^{.9467}$
Bizygomatic breadth	$Y = .4608X^{.8179}$	$Y = .2864X^{.9180}$	$Y = .1986X^{.9597}$

C. VARIABILITY DURING DEVELOPMENT

Biological variation between individuals is not uncommon during development and growth. The extent and causes of this variation are examined in this section.

1. DIFFERENTIAL DEVELOPMENT OF EXTERNAL FEATURES

In order to detect and assess any variation between rates of development in different morphological regions, a representative group of animals was selected for study. This included fetuses ranging from individuals with very little body hair covering to those with a thick coat of hair.

The sequence of changes in several regions during development is outlined as reconstructed after examining a series of 37 fetuses. The rates of development are then compared between each region.

1. Growth of hair on the anterior lateral sides of the rostrum

Hair emerges in this region later than on adjacent areas and later than on many regions of the body. Skin may be readily observed here when skin is obscured by hair growth elsewhere. Progressive levels of development may be readily distinguished by observing the amount of hair present in different animals.

2. Growth of hair on the dorsal surfaces of the auricles of the ears

Not only is the progressive appearance of hair in this region a suitable indicator of development, but as the hair grows a colour change occurs as new bands emerge. The dorsal surfaces of the auricles appear black when hair first emerges, but become progressively more brown or red at higher levels of development.

3. Growth of hair on the mid-dorsal region of the trunk between the dorsal-most rows of white trunk spots

The pelage in this region first appears as a few well-spaced isolated hairs. As development proceeds, the hairs become more dense and eventually obscure the underlying skin. The dorsal trunk first appears black but changes to brown as the hairs emerge from a velvet-like covering to a thick woolly covering.

4. Growth of hair from the white trunk spots

The white hairs that grow from the trunk spots first appear later than the dark-coloured hairs of the back. When the hair lies flat along the back of the animal, relative growth of

the trunk spot hairs may be estimated by observing the degree of proximity of adjacent spots. Animals having well-defined spots with short white hairs may be distinguished from those at higher levels of development with trunk spots composed of long tufts of white hair.

5. Growth of hair on the dorsal surface of the tail

When the hair on the back and tail is first emerging, the colour of both these regions is black. Part of the tail is always black during the growth of the fetus, but when the hair of the proximal region of the tail and the back reaches a certain length it has a brown appearance.

6. Growth of the white hair on the posterior ventral surface of the abdomen and the medial surfaces of the legs

The growth of hair in this region advances from stages in which sparse but long white hairs are present to animals exhibiting a thick growth of hair that obscures even the male genital organs.

7. Growth of hair in the region of the tarsal gland

In early stages the skin of the tarsal gland is easily visible. As growth proceeds, the gland surface becomes covered

in short hairs. Longer white hairs border the gland but do not obscure the central region. Upon further development, the peripheral white hairs hide the gland and eventually the region takes on a thick woolly appearance.

8. Growth of hair on the hind feet

Hair growth on the hind feet is slower than that on the front feet. The hind feet appear grey before much hair has emerged, take on a black appearance when covered in short hair, and become brown as the hair grows. The central region of the metatarsal gland, although not itself covered with hair, becomes obscured by peripheral hair in older animals. One animal was found to have hair growing from the central glandular region.

9. Development of the nasal pigmentation

The inferior nasal pigmentation develops more slowly than the superior nasal pigmentation. It is therefore lighter in colour than the superior nasal pigmentation during much of the gestation, but in the final stages of development the two areas of pigment are the same black colour. Fetuses may conveniently be sequentially grouped as follows: (a) those in which the inferior nasal pigmentation is mid-brown in colour

and readily distinguishable from the darker superior nasal pigment; (b) those in which the inferior nasal pigmentation is dark brown or grey in colour and difficult to distinguish from the superior nasal pigment; (c) those in which the two areas of pigment are confluent as one region of nasal pigmentation. Most animals have white spots on their nasal pigment during growth. White spots have been observed at all levels of development but in the series of 37 animals examined, spots were less prevalent in the later stages. White spots were absent from the superior nasal pigment in 7.1% of the animals that could be classified as group (a), 22.2% of those in group (b), and 28.5% of those in group (c).

10. Development of the teeth

Incisors and canines may be distinguished under the periodontal membrane long before they erupt. Eruption appears to proceed from the lateral sides. Different levels of tooth development are readily distinguished.

Using the preceding data as a basis of comparison, the fetuses were arranged in order, least developed to most developed, with respect to only one morphological region at a time (single-trait rank orders). Thus the series was arranged in developmental

order 10 times. The position (rank) in the series that a given fetus was assigned on the basis of development in one region can be compared to the rank it was assigned for development in another region.

The results of ranking the animals in accordance with the level of development of each of the preceding characteristics may be seen in Table V. When it was impossible to assign a different rank to each fetus in a group, they were all given the middle value of the ranks they would be assigned if they could be distinguished.

It is evident just from scanning the table that not all regions develop at comparable rates in all animals. This is further illustrated by values obtained using Spearman's measure of rank correlation. For example, a correlation of .57 is found between the growth of hair on the anterior lateral sides of the rostrum and on the dorsal surfaces of the auricles of the ears. A correlation of only .21 is obtained for the growth of hair on the rostrum and the development of the inferior nasal pigment. This situation presents an interesting problem when attempting to relate structure to fetal age. The use of any combination of characters to assess age is obviously limited, and complicated by the fact that there is greater variation between rates of development in some features than in others.

It may be noted, however, that a given fetus has often been assigned to a similar rank for a number of characteristics. Animal number 15, for example, is ranked no higher than 19 and no lower than 9.5 for any area of development. Thus limits may be set for the recognition of distinct stages in development, as was outlined in a preceding section. The true developmental sequence (age order) of the animals in this series may likewise be approached within limits. A workable estimate of the level of development of each fetus that may approximate true age in terms of structural development has been obtained by calculating the mean rank of each animal.

In reference to these results, it is interesting to note that size alone cannot be relied upon as a precise indicator of age, as is discussed in another section.

TABLE V

COMPARISON OF DEVELOPMENT OF 10 DIFFERENT REGIONS

Fetus No.	Ranks assigned to each fetus for level of development in 10 regions										Mean Rank
	*1	2	3	4	5	6	7	8	9	10	
1	3	2	2	2.5	1	1.5	2	1.5	2	1	1.85
2	3	1	1	2.5	2	1.5	2	1.5	3	4	2.05
3	3	4	4	2.5	4	4	3	4	1	2	3.15
4	3	3	3	2.5	3	3	4	3	4	3	3.15
5	3	5	5	5	5	6	5	5	5	6	5.0
6	6	6	6	6	6	5	6	6	6	5	5.8
7	7	7	25.5	7	9.5	12.5	7	7	19	15.5	11.7
8	11	9	10	8	9.5	12.5	17	9	10	15.5	11.15
9	14	11	10	11	9.5	12.5	17	17	7	15.5	11.95
10	8	8	10	9	9.5	12.5	9	8	30.5	15.5	12.0
11	12	12	10	14	9.5	12.5	17	11	11	15.5	12.45
12	10	14	10	13	25	12.5	13	10	8	25.5	13.5
13	15	13	10	12	9.5	12.5	17	13	19	15.5	13.65
14	9	10	25.5	10	25	12.5	17	10	9	15.5	14.35
15	12	15	25.5	21	25	12.5	8	16	18	15.5	17.05
16	16	20	25.5	21	25	12.5	17	15	12	15.5	17.95
17	19	17	25.5	21	25	12.5	10	17	19	15.5	18.15
18	30	18	11	21	25	12.5	12	18	30.5	15.5	19.35
19	17	19	25.5	21	25	23	17	23	19	15.5	20.50
20	30	16	25	21	25	23	24	23	13	15.5	21.06
21	18	21	25.5	21	25	23	11	23	30.5	15.5	21.35
22	20	25	25	21	25	23	24	23	19	15.5	22.10
23	30	23	25	21	25	23	24	23	14	15.5	22.40
24	21	24	25	21	25	23	24	23	19	25.5	23.10
25	22	22	25.5	21	25	23	24	23	30.5	15.5	23.15
26	30	31	25	21	25	23	24	23	19	28.5	25.05
27	30	31.5	25.5	21	25	23	24	23	30.5	25.5	25.90
28	30	31.5	25.5	32.5	25	32.5	32.5	32.5	19.0	33.5	29.45

* Numbers in this horizontal row correspond to the numbers assigned to regions described in text.

TABLE V (continued)

Fetus No.	Ranks assigned to each fetus for level of development in 10 regions										Mean Rank
	*1	2	3	4	5	6	7	8	9	10	
29	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	27	29.95
30	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	28.5	30.05
31	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60
32	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60
33	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60
34	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60
35	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60
36	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60
37	30	31.5	25.5	32.5	25	32.5	32.5	32.5	30.5	33.5	30.60

2. DEVELOPMENT OF TWINS AND TRIPLETS

A series of 28 sets of twins was examined in detail, to compare the levels of structural development within each pair. A maximum of 12 characteristics were evaluated as a basis for any single comparison. In at least 19 sets of twins, one member appeared to be structurally more advanced (have a higher mean rank) than the other. Some animals differed with respect to only one characteristic, but others were considered more advanced in as many as seven.

Each member of the set of triplets examined was considered to be at a different level of development on the basis of the characters used for assessment.

In no case was it necessary to assign an animal to a stage different from that of its siblings.

3. SEX DIFFERENCES

Fetuses were examined to detect possible differences in rates of development between males and females. The specimens were compared with regard to degree of morphological development (mean rank), sex and size. The criterion adopted was such that if members of one sex were usually larger than members of the

opposite sex of equal or higher mean rank, this would suggest possible sex-specific growth rates.

Twins were evaluated on the assumption that each member of a pair is the same developmental age. Size comparisons of animals were based on forehead-rump and calcaneus-hoof lengths.

Of eight sets of twins of mixed sex in which one member of each set was considered to be structurally more developed than the other, the male was more developed than the female in four sets, and the female was more developed than the male in four sets. However, of a total of 15 pairs of mixed sex, the male had a greater calcaneus-hoof length in every case and a greater forehead-rump length in 12 cases.

To obtain further information, it was necessary to make comparisons other than within sets of twins. A sample of 40 animals was selected including only fetuses that were developed to such an extent that relatively significant morphological comparisons could be made between them. To simplify size comparisons, no animal was considered "larger" than another unless both measurements of size exceeded those of the other animal. The following relationships were evaluated and are represented in the table.

1. In comparing male and female singletons, one case was found in which two males ("a" and "e" in Table VI) were larger than a female ("f") considered to be morphologically more developed (of higher mean rank) than either male. Conversely, no situation was found in which a female singleton was larger than a structurally more developed male.
2. One case was discovered in which a male singleton ("e" in Table VI) was larger than morphologically more developed female twins ("g" and "h" in Table VI). There was no instance of a female singleton larger than a more developed male twin.
3. Several male twins were found to be larger than female singletons of equal or greater morphological advancement. (In the table, male twins "b," "c" and "d" are all larger than more structurally advanced female singleton "f.") No female twin was found that was larger than a structurally more developed male singleton.

Thus there appears to be a tendency for male size dominance in the specimens available. Male twins tend to be larger than more developed female twins. Male singles are larger than more developed female singles. Male singles are larger than more developed female twins. Male twins are larger than more developed female singles.

It is apparent therefore that males tend to be larger than females at each stage when due consideration is given to the developmental circumstances.

TABLE VI
THE RELATIONSHIP BETWEEN SIZE, SEX AND LEVEL
OF DEVELOPMENT IN A GROUP OF FETUSES

Fetus	Developmental rank (least developed to most developed)	Forehead-rump length (mm.)	Calcaneus-hoof length (mm.)
a. Male singleton	1	328.5	142.5
b. Male twin	2	321.0	147.5
c. Male twin	3	346.0	154.5
d. Male twin	4	335.0	151.0
e. Male singleton	5	355.0	154.0
f. Female singleton	6	309.5	140.0
g. Female twin	7	334.0	150.5
h. Female twin	8	330.0	150.5
i. Male twin	9	386.0	192.0
j. Female singleton	10	366.0	176.0
k. Male twin	11	448.0	232.5
l. Female singleton	11	436.0	216.0

4. THE RELATIONSHIP BETWEEN SIZE AND FORM

A number of animals were studied in order to estimate the degree of correlation between morphological changes and body dimensions. For the purposes of this study, animals were segregated with regard to sex, number in the uterus (twin or single), and year of capture. Any variation caused by sex differences, uterine environment, or environment of the mother, was therefore eliminated as well as possible. Fetuses in each group were arranged according to their estimated level of morphological development (mean rank). They were also ranked in size order, in terms of forehead-rump length, bizygomatic breadth, calcaneus-hoof length, ear length and ventral tail length. All are measurements that can be taken with some degree of precision, and thus are possibly useful as indices of development.

Morphological development was compared to each of these appraisals of fetus size using Spearman's measure of rank correlation. In no group was a perfect correlation obtained. The different values obtained for the different measurements probably reflect, in part, the accuracy with which they may be taken. The highest correlation of all was obtained between calcaneus-hoof length and estimated level of structural development. Indeed, this is a measurement that can be taken with greater precision than any, and probably resists postmortem changes as well as any.

TABLE VII

DEGREE OF CORRELATION BETWEEN MORPHOLOGICAL
DEVELOPMENT AND VARIOUS DIMENSIONS

Group	Developmental rank (least developed to most developed)	Size rank (smallest to largest)				
		FR	CH	BZB	EL	VT
Male twins 1964	1	1	1	4.5	6.5	8
	2	7	3	6	1	1
	3	3	2	2	2	2
	4	2	4	7	4	3
	5	6	6	4.5	6.5	4
	6	4	7	1	5	5
	7	5	5	3	3	7
	8	8	8	8	7	6
Correlation with developmental rank		.55	.95	.19	.50	.31
Female twins 1964	1	5	4	1	3	2
	2	1	1	2	1	4
	3	3.5	2.5	3	2	1
	4	2	2.5	5.5	4	3
	5	3.5	5	4	5	5
	6	7	7	8	7	8
	7	6	6	5.5	6	7
	8	8	8	7	8	6
Correlation with developmental rank		.67	.82	.88	.95	.83

NOTE: FR=Forehead-rump length; CH=Calcaneus-hoof length; BZB=Bizygomatic breadth; EL=Ear length; VT=Ventral tail length.

TABLE VII (continued)

Group	Developmental rank (least developed to most developed)	Size rank (smallest to largest)				
		FR	CH	BZB	EL	VT
Male singletons 1966	1	2	2	4	4	2.5
	2	1	1	1	1	1
	3	3	3	2	2	4
	4	4	4	5	5	5
	5	5	5	3	3	2.5
Correlation with developmental rank		.90	.90	.35	.55	.35

DISCUSSION

This investigation outlines some aspects of the development of the Columbian black-tailed deer fetus. The sample size is small and the results can only be considered suggestive.

1. TECHNICAL PROBLEMS IN STUDYING DEVELOPMENT

Preservation of material

Many investigators studying growth in wild populations rely on data obtained from preserved material. It is well known, however, that preservation of fetal material in various fluids may cause changes in the dimensions after a period of time. Also, it is evident from the results that great variation may occur between the reactions of different dimensions, different animals and different size groups of animals. Similar variation has been observed by other investigators (e.g., Scammon and Calkins, 1925; Joubert, 1956).

Although most of the changes resulting from preservation are not significant, they are variable, difficult to explain and difficult to predict. For these reasons it is suggested that if fine results are required, fetuses should be measured before preservation.

Selection of measurements

The results of this and other investigations (e.g., Todd, 1925) show that the selection of external measurements that attempt to represent dimensions between subcutaneous bony points has limitations. The most accurate and most precise measurements are probably those involving bony reference points with the least amount of soft tissue covering. These are more useful for studying growth due to their greater accuracy and more useful for field work due to their precision. Human error is probably greater for less easily defined reference points. Also, soft tissue does not seem to resist changes caused by formalin preservation as well as bone resists them.

2. FETAL MATERIAL

Sampling for growth: material of unknown age

Certainly the most accurate and complete method of studying development is to describe and measure a series of live animals over a period of time as each reaches a series of known ages. Environmental factors that influence growth can be controlled, and a series of individual records can be obtained as

well as a series of population means. This method is difficult to apply to most wild populations and nigh impossible to use for intra-uterine development. In this study the population was not only wild but also intra-uterine. The ages of the specimens were unknown, the environment was not controlled, and all the specimens were not collected in the same season. Nevertheless, sequential sampling of a population of unknown-age individuals may provide much data. These data may not be useful in studying absolute growth, but are invaluable in studying relative growth and differentiation, both treated here.

Known-age specimens

Material of unknown age may become more meaningful if related to some specimens of known age. Using specimens of which the age is known, it is possible to determine how certain dimensions change in relation to time. Inferences may then be made regarding the relationship between unknown-age material and time. (If this relationship is assumed when studying absolute growth rates of unknown-age material, then one is assuming that which he is attempting to prove.)

An effective technique for obtaining known-age fetuses has been described. The occurrence of estrus in the doe can be detected in a very short time by assessing two behavioral

situations: the reaction of the isolated animal to the investigator and the interaction between the buck and doe when placed together in the same pen. Using this same system, a larger series of known-age animals could possibly be obtained with success. In contrast to a system such as that described by Browman and Hudson (1957), a minimal expenditure of time is required and the animals concerned are saved much physical and emotional distress. The animals may be kept under carefully controlled conditions and individual records may be maintained with regard to such factors as food and water consumption. Social interaction may be regulated accordingly. The short duration of estrus observed in this study is a great advantage in obtaining material of accurate age.

3. PATTERNS OF DEVELOPMENT

This study has attempted to reconstruct the probable sequence and patterns of change in form and size during the fetal period. Development, however, is a composite of dynamic biological processes occurring in the living animal. The specimens available for study were not living, a common situation in research problems of this nature. The patterns of development

that have been described must therefore be treated as purely inferential.

External form

A series of stages have been described to outline the sequential development of the external form of the fetus. These stages are purely subjective, created only as a convenient means of dealing with the material available for study. When more material becomes available, a more detailed outline, including more stages, can be made.

The pattern of fetal development is similar to that described for other species of mammals. The typical stages in the fetal period are represented, including the characteristic eyelid growth, periderm sealing and periderm resorption. The sequence of hair emergence demonstrates a cephalocaudal growth gradient.

It is difficult to compare the fetal development of this species to others, as most studies express development as a function of time. Comparisons based on absolute size are probably inaccurate, since techniques of preservation differ between investigators. However, relationships will be discussed between fetal development in the Columbian black-tailed deer, the Rocky Mountain mule deer and the Northern white-tailed

deer. Information on the latter two forms is taken from Armstrong (1950) and Hudson (1956).

In many regions structural changes appear to have occurred at a smaller size in the blacktail than in the other deer. For example, metatarsal glands are evident in the blacktail at a forehead-rump length of 103.2 mm. They are evident in the mule deer at a forehead-rump length of 110.7 mm. and in the whitetail at 168 mm. The white trunk spots appear in the blacktail by 229 mm., in the mule deer by 327 mm. and in the whitetail by 235 mm. Hair appears on the limbs of the blacktail, mule and whitetail by 226 mm., 252 mm. and 270 mm. respectively. Incisors erupt at 385 mm., 397 mm. and 441 mm. in the three forms. Hudson (1959) found sex determination rather difficult and uncertain in mule deer fetuses smaller than 70 mm. No difficulty was encountered sexing blacktail fetuses as small as 45.2 mm. in this study.

The known-age specimens available suggest that white-tailed deer and mule deer fetuses grow faster than blacktails. Indeed, if patterns of development are more closely related to time than to size, this may explain some of the variation observed in the preceding examples. However, different growth rates, techniques of preservation and incomplete series of specimens probably do not account for all the variation observed.

Greater variation is seen in the development of other features. For example, nasal pigment is first apparent in the whitetail by 114 mm., in the mule deer by 110.7 mm. and in the blacktail by 126 mm. The sagittal suture becomes "distinct" in the mule deer at 59.2 mm. and "obvious" in the whitetail at 46 mm. The sagittal suture becomes neither distinct nor obvious in the blacktail until a much greater size is reached and a large anterior fontanelle exists well after hair covers the body surface (300 mm.).

In summary then, the sequence of development appears similar in the different forms of deer. Most structural changes tend to occur at a smaller size in the Columbian black-tailed deer than in the other forms. In some cases this may be explained by differences in absolute rates of growth.

Growth

Careful consideration must be given to interpretation of the data on growth. When studying allometric growth between different kinds of tissues in the fetus, the maternal plane of nutrition must be considered. Different fetal tissues and organs respond to poor nutrition in different ways. The growth relationships described between weight and length may be useful in comparing intra-specific populations. Most of the growth

patterns described, however, reflect mainly growth in the skeleton. According to Wallace (1948), the pattern of development within one kind of fetal tissue (e.g., bone) is the same in slowly or rapidly growing sheep fetuses (low or high plane of maternal nutrition). If this applies to deer, then the patterns of growth described here will likewise be little affected by the nutrition of the doe and in this sense will be of more value in indicating genetic differences between populations than would time-related growth patterns.

Fetal growth patterns of the Columbian black-tailed deer have been compared to those of the Northern white-tailed deer and Rocky Mountain mule deer after examining and statistically testing the data of Armstrong (1950) and Hudson (1956). Growth has been compared on the basis of forehead-rump length using six morphological regions, namely the cranium, neck, chest, abdomen, forelegs and hind legs.

In both the blacktail and mule deer the neck grows relatively faster in circumference than the abdomen ($P < .01$) and the hind legs grow relatively faster than the forelegs ($P < .01$). In the whitetail, the differences in growth between the neck and abdomen and between the hind legs and forelegs are not significant.

In most cases the growth patterns of the mule deer are not significantly different from those of the blacktail. The bizygomatic breadth increases relatively faster ($P < .01$) in the mule deer.

Several regions of the whitetail appear to have different growth patterns than corresponding regions of the blacktail. In relation to forehead-rump length, the hind leg of the whitetail grows more slowly ($.01 < P < .05$). Regions that grow relatively faster in the whitetail are the median neck circumference ($P < .01$), abdomen circumference ($.01 < P < .05$) and bizygomatic breadth ($P < .01$).

4. VARIATION IN DEVELOPMENT

Individual variation

As is evident from the results, considerable individual variation occurs between fetuses in the rate of development of one region compared to another. It is possible that this variation may be wholly or partially attributed to genetic differences in regional differentiation rates. As Kraus and Choi (1958) point out, in the skeletal system alone, it is possible that there is regional genetic control (in addition to the general field of genetic influence) in prenatal bone growth.

Sex ratio

The sex ratio of the fetuses of determinable sex was 38 females to 46 males. This is in contrast to the ratio observed by Hudson (1959) of 100 females to 87 males in mule deer. Downing (1965) described a situation in white-tailed deer in which fawns were produced in a ratio of 24 males to 6 females by a breeding population of nearly even sex ratio. He offered the suggestion that the first service of a buck each year may produce predominantly male offspring, while subsequent matings produce predominantly female offspring (assuming, in this case, that few bucks bred more than one doe).

Sex differences

The results of this study suggest that the male fetus grows faster (at least at some time during development) than the female fetus. Armstrong (1950), using weight and age as criteria, reached the same conclusion regarding white-tailed deer. She found that males were heavier than females of the same age, but female singletons were heavier than male twins. In the current study, male twins were found to be larger than female singles. These determinations were based on length and rank, however. Donald and Purser (1956) observed male size

dominance in twin lambs of mixed sex and suggest that the male fetus may be able better to compete for some element in short supply in the intra-uterine environment. Hudson (1959) examined 17 sets of fetal mule deer twins and found no significant tendency for either sex to dominate in either weight or forehead-rump length.

Litter size

The number of single, twin and triplet fetuses was found to be 23, 31 and one (41.8%, 56.3% and 1.8%). Hudson (1956) reports mule deer recoveries of singles, twins, triplets and quadruplets to be 23.8%, 67.7%, 6.3% and 2.1%. Morton and Cheatum (1946) have suggested that variation in litter size of two white-tailed deer populations studied was related to geographic variation in availability of essential nutrients. The number of singles, twins and triplets of the more productive population was of the ratio 3:6:1. The other population was 8:2:1. Verme (1965) subjected pregnant white-tailed deer to different planes of nutrition during October and November (during or prior to ovulation). The ratio of singles, twins and triplets was 2:21:1 for animals on an excellent diet, 17:2:0 for animals on a poor diet. Animals on both diets were fed pellets containing 12% protein with 1,250 digestible

calories per gram. Deer on the high nutrition diet received approximately 3.5 pounds of ration per animal per day. Animals on the low plane of nutrition were each fed 2.5 pounds per day in October and 1.5 pounds daily in November.

Twin development

The degree of development of external characteristics was found to be different within every pair of fetal twins of mixed sex studied. Armstrong (1950) examined 11 sets of mixed twins of white-tailed deer fetuses and found the degree of development to be the same within each set.

Variation in general

Variation during prenatal development is common between individuals and between populations. Many factors have been observed to influence the development of the fetus in various species of mammals. These include the maternal and paternal genotypes (Castle and Gregory, 1929; Gregory and Castle, 1931), maternal size (Foote et al., 1959; Hunter, 1956; Joubert and Hammond, 1958), maternal age (Dickinson et al., 1962), maternal nutrition (Wallace, 1948), parity of the mother (McKeown and Record, 1953), sex of the fetus (Donald and Purser, 1956),

litter size (Wishart and Hammond, 1933), placental size (Eckstein et al., 1955), and ambient temperature (Yeates, 1958).

The current investigation has mainly been concerned with describing the basic pattern of development of the fetus. A useful appraisal of the causes of variation in development can only be made in future studies using controlled experiments.

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APPENDIX

FIGURE 1

RELATIONSHIP BETWEEN
WEIGHT AND FOREHEAD-RUMP LENGTH

FIGURE 2

RELATIONSHIP BETWEEN
EAR LENGTH AND FOREHEAD-RUMP LENGTH

FIGURE 3

RELATIONSHIP BETWEEN
CALCANEUS-HOOF LENGTH AND FOREHEAD-RUMP LENGTH

FIGURE 4

RELATIONSHIP BETWEEN
LENGTH OF HIND LEG AND FOREHEAD-RUMP LENGTH

FIGURE 5

RELATIONSHIP BETWEEN
LENGTH OF FORELEG AND FOREHEAD-RUMP LENGTH

FIGURE 6

RELATIONSHIP BETWEEN
LENGTH OF FEMUR AND FOREHEAD-RUMP LENGTH

FIGURE 7

RELATIONSHIP BETWEEN
LENGTH OF HUMERUS AND FOREHEAD-RUMP LENGTH

FIGURE 8

RELATIONSHIP BETWEEN
LENGTH OF THE INNOMINATE BONE AND FOREHEAD-RUMP LENGTH

FIGURE 9

RELATIONSHIP BETWEEN
VENTRAL TAIL LENGTH AND FOREHEAD-RUMP LENGTH

FIGURE 10

RELATIONSHIP BETWEEN
CHEST CIRCUMFERENCE AND FOREHEAD-RUMP LENGTH

FIGURE 11

RELATIONSHIP BETWEEN
CRANIAL LENGTH AND FOREHEAD-RUMP LENGTH

FIGURE 12

RELATIONSHIP BETWEEN
PREOPTIC LENGTH AND FOREHEAD-RUMP LENGTH

FIGURE 13

RELATIONSHIP BETWEEN
MEDIAN NECK CIRCUMFERENCE AND FOREHEAD-RUMP LENGTH

FIGURE 14

RELATIONSHIP BETWEEN
ABDOMEN CIRCUMFERENCE AND FOREHEAD-RUMP LENGTH

FIGURE 15

RELATIONSHIP BETWEEN
HIP WIDTH AND FOREHEAD-RUMP LENGTH

FIGURE 16

RELATIONSHIP BETWEEN
TRANSVERSE CHEST DIAMETER AND FOREHEAD-RUMP LENGTH

FIGURE 17

RELATIONSHIP BETWEEN
BIZYGOMATIC BREADTH AND FOREHEAD-RUMP LENGTH

FIGURE 18

RELATIONSHIP BETWEEN
INTERORBITAL BREADTH AND FOREHEAD-RUMP LENGTH

FIGURE 19

RELATIONSHIP BETWEEN
WEIGHT AND CALCANEUS-HOOF LENGTH

FIGURE 20

RELATIONSHIP BETWEEN
EAR LENGTH AND CALCANEUS-HOOF LENGTH

FIGURE 21

RELATIONSHIP BETWEEN
LENGTH OF HIND LEG AND CALCANEUS-HOOF LENGTH

FIGURE 22

RELATIONSHIP BETWEEN
LENGTH OF FORELEG AND CALCANEUS-HOOF LENGTH

FIGURE 23

RELATIONSHIP BETWEEN
LENGTH OF FEMUR AND CALCANEUS-HOOF LENGTH

FIGURE 24

RELATIONSHIP BETWEEN
LENGTH OF HUMERUS AND CALCANEUS-HOOF LENGTH

FIGURE 25

RELATIONSHIP BETWEEN
LENGTH OF THE INNOMINATE BONE AND CALCANEUS-HOOF LENGTH

FIGURE 26

RELATIONSHIP BETWEEN
VENTRAL TAIL LENGTH AND CALCANEUS-HOOF LENGTH

FIGURE 27

RELATIONSHIP BETWEEN
CHEST CIRCUMFERENCE AND CALCANEUS-HOOF LENGTH

FIGURE 28

RELATIONSHIP BETWEEN
CRANIAL LENGTH AND CALCANEUS-HOOF LENGTH

FIGURE 29

RELATIONSHIP BETWEEN
PREOPTIC LENGTH AND CALCANEUS-HOOF LENGTH

FIGURE 30

RELATIONSHIP BETWEEN
MEDIAN NECK CIRCUMFERENCE AND CALCANEUS-HOOF LENGTH

FIGURE 31

RELATIONSHIP BETWEEN
ABDOMEN CIRCUMFERENCE AND CALCANEUS-HOOF LENGTH

FIGURE 32

RELATIONSHIP BETWEEN
HIP WIDTH AND CALCANEUS-HOOF LENGTH

FIGURE 33

RELATIONSHIP BETWEEN
BIZYGOMATIC BREADTH AND CALCANEUS-HOOF LENGTH

FIGURE 34

RELATIONSHIP BETWEEN
TRANSVERSE CHEST DIAMETER AND CALCANEUS-HOOF LENGTH

FIGURE 35

RELATIONSHIP BETWEEN
INTERORBITAL BREADTH AND CALCANEUS-HOOF LENGTH

FIGURE 36

RELATIONSHIP BETWEEN
INTERORBITAL BREADTH AND BIZYGOMATIC BREADTH

FIGURE 37

RELATIONSHIP BETWEEN
EAR LENGTH AND BIZYGOMATIC BREADTH

FIGURE 38

RELATIONSHIP BETWEEN
PREOPTIC LENGTH AND CRANIAL LENGTH

FIGURE 39

RELATIONSHIP BETWEEN
CHEST CIRCUMFERENCE AND ABDOMEN CIRCUMFERENCE

FIGURE 40

RELATIONSHIP BETWEEN
TRANSVERSE CHEST DIAMETER AND HIP WIDTH

FIGURE 41

RELATIONSHIP BETWEEN
HIP WIDTH AND LENGTH OF INNOMINATE BONE

FIGURE 42

RELATIONSHIP BETWEEN
LENGTH OF FORELEG AND LENGTH OF HUMERUS

FIGURE 43

RELATIONSHIP BETWEEN
LENGTH OF HIND LEG AND LENGTH OF FEMUR

FIGURE 44

RELATIONSHIP BETWEEN
LENGTH OF FEMUR AND LENGTH OF HUMERUS