


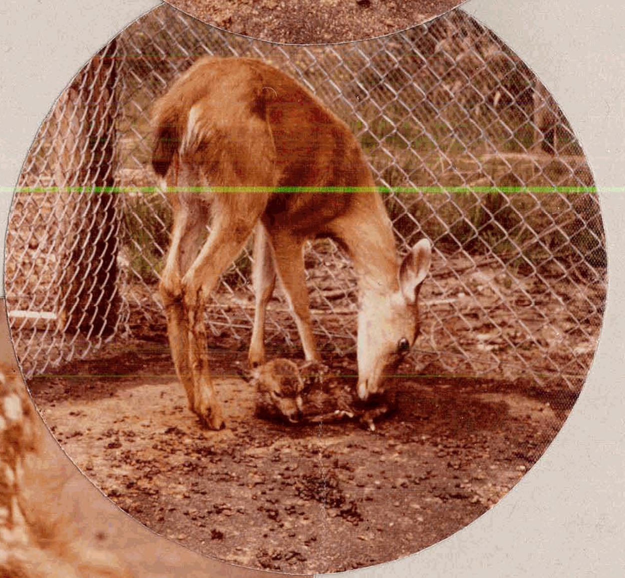


AN INVESTIGATION OF PRECOCIOUS PUBERTY IN CAPTIVE FEMALE BLACK-TAILED DEER (*Odocoileus hemionus columbianus*)

by

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ABSTRACT

This study on puberty of female fawns in a captive herd of black-tailed deer was carried out from 1973 to 1976. The stock largely originated from fawns collected from the wild at Kelsey Bay on Vancouver Island, British Columbia.

Wild-caught fawns were hand-raised on evaporated milk and fed after weaning on a high protein diet (one exception: 6 experimental fawns in 1975 on low protein diet). Body weights and measurements were recorded at short intervals. The age of wild-caught fawns was estimated from the capture weight using a regression formula of weight on age developed from fawns of known age.

No differences were found in the growth of hand-raised and mother-raised fawns (born in the enclosure) which were, therefore, counted together when precocious and non-precocious fawns were compared.

Puberty attainment was determined by the subsequent occurrence of parturition, except in 1976/77 when x-ray examination was used. Precocious puberty was seen in all years in a proportion of female fawns on high protein diets: 13/20, 1973; 3/7, 1974; 1/4, 1975; 5/7, 1976. Thus an average of more than half of these fawns showed precocious puberty. In contrast none of 6 fawns on a low protein diet (in 1975) attained puberty despite weight gains similar to fawns on high protein diets. Precocious fawns were significantly heavier than non-precocious fawns at 125, 175 and 225 days of age. Growth patterns up to the inflection point of the weight growth curves and weights at 25 and 75 days of age were not different between the two groups. However,

the weight at the end of the breeding season, in percent of the adult weight, was significantly higher in precocious fawns.

During the breeding season, the average weight of experimental fawns (both precocious and non-precocious) was significantly higher than the average weight of wild fawns. Despite this statistical difference, there was considerable overlap in the range of individual weights between wild and experimental fawns. Thus weight influences the attainment of puberty but each animal has its own, individual critical weight at which puberty is achieved within a defined, species-specific range.

It is therefore postulated that the absence of puberty in wild female black-tailed deer fawns is due to insufficient protein supply before and during the season at which the necessary photoperiodic conditions exist. As feed protein content affects puberty attainment indirectly through its influence on weight growth and directly through its effect on the endocrine system, an insufficient supply of this nutrient can effectively prevent puberty. This postulate is based on the differences in puberty attainment between fawns on high and low protein diets observed in this study, and on published observations of deer and sheep which describe the role of protein supply in weight achievement and endocrine function.

So uebt Natur die Mutterpflicht
Und sorgt, dass nie die Kette bricht
Und dass der Reif nie springet.
Einstweilen, bis den Bau der Welt
Philosophie zusammenhaelt,
Erhaelt sie das Getriebe
Durch Hunger und durch Liebe.

Friedrich von Schiller

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INTRODUCTION

The period of life at which reproduction first becomes possible for young mammals is known as puberty (Asdell, 1964). It is usually reached at a typical age for each species, although its achievement can be influenced by many factors such as nutrition, season of birth and sociological factors (Sadleir, 1969; Perry, 1971). Puberty is characterized by the release of viable gametes from the gonads and an increased level of circulating estrogens or androgens. The latter phenomenon is responsible for the appearance or the development of the secondary sexual characters. Although animals are capable of reproduction at puberty, they usually only reach their full reproductive capacity some time later when they become sexually mature (Crew, 1931; Perry, 1971).

The time of the year at which an individual reaches puberty depends on whether or not it belongs to a seasonally breeding species. In non-seasonal breeders, puberty can be reached at any time of the year. In seasonally breeding species, young reach puberty at that time of the year which is characterized as the breeding season for that species in that locality. In addition, the attainment of puberty is influenced by environmental factors (Sadleir, 1969).

Within the family Cervidae, there are both seasonal and non-seasonal breeders. Tropical species such as *Axis axis* (Chital) and *Muntiacus muntjak* (barking deer) can breed at any time of the year (Asdell, 1964; Whitehead, 1972), but most deer have well defined breeding seasons — especially those inhabiting northern latitudes (Table I). In the two species of the genus Odocoileus, namely O. virginianus (white-tailed deer) and O. hemionus (O.h. hemionus - mule deer, O.h. columbianus - Columbian black-tailed deer, O.h. sitkensis - Sitka deer: Cowan and Guiget, 1965) the rut takes place in fall, usually from November to December. There are variations between the subspecies, however, and generally breeding occurs somewhat earlier in the southern range of the genus and later in the north (Adams, 1960; Cheatum and Morton, 1946; Chattin, 1948; Dasmann and Taber, 1956; Rust, 1946; Thomas, 1970). Brown (1961) found that in western Washington the peak of breeding of the Columbian black-tailed deer occurred between November 10th and 25th from 1949 to 1954, and was only delayed for ten days by a cold spell in 1955.

This, then, is also the time of the year at which puberty is reached by the young deer (Table I), although they often breed towards the end of the season: e.g. in New York State and in Iowa white-tailed does breed in their first year but about 2 to 4 weeks later than the adults (Asdell, 1964; Jackson and Hesselton, 1971; Haugen, 1975), whereas in southern Illinois 1 year olds breed 4 to 5 weeks later than older does (Roseberry and Klimstra, 1970). Thomas (1970) noted that yearlings of Columbian black-tailed deer on Vancouver Island bred later than adults, and in an Oregon herd, yearlings were the last to breed every year (Hines, 1968). Taber (1953) stated that yearling black-tailed deer in California breed later than adults, and

Table I - Age at puberty and breeding season of deer (subfam. *Cervinae*)

Species	Puberty	Rut
Fallow (*Dama dama*) (1)	31 months, some earlier	September - late October
Red (*Cervus elaphus*) (1)	females usually 3rd year males towards 4th year, - from end of 2nd year	August - October (depending on area)
Thamin (*C. eldi*) (1)	18 months	March to May (in Burma)
Rusa (*C. timorensis*) (1)	Females 27 months	June to September
Sika (*C. nippon*) (1)	Between 16 - 18 months	September to mid October
Moose (*Alces alces*) (1)	16-28 months, most males 2 1/2 years	mid September to mid October
Black-tailed (2, 3, 4) (*O.h. columbianus*)	as yearlings, some not until 2 1/2 years old	October - January (Peak November)
White-tailed (3, 5, 6, 7, 8, 9) (*O. virginianus*)	at 6 to 7 months relatively common, most at 1 1/2 years	November to December

(1) Asdell, 1964
(2) Cowan, 1956
(3) Brown, 1961
(4) Thomas, 1970
(5) Cheatum and Severinghaus, 1950
(6) Trainer, 1962
(7) Ransom, 1967
(8) Roseberry and Klimstra, 1970
(9) Haugen, 1975

Swank (1958) observed the same phenomenon in Arizona mule deer.

The age at which puberty is attained in the *Cervidae* differs from species to species, and can vary greatly within the same species (Table I). One reason for this great variation is the seasonality of breeding in most deer. If a young of these species does not reach puberty during the first breeding season of its life, it has to wait a full year for the second season. Normally none of the true deer (*Cervinae*) reach puberty earlier than in the second year of their life, although under certain field conditions small numbers of individuals may breed earlier. An exception to this statement is the white-tailed deer: it frequently breeds in the first fall of its life (Table II). Daniel (1963) reported that in New Zealand, introduced Javan rusa (*C. timorensis*), Ceylon sambar (*C. unicolor*) and red deer (*C. elaphus*) can reach puberty at about 6 months of age when feeding on clover and alfalfa fields. These species usually breed when 2 years old.

In mule deer (*O. h. hemionus*) the fact that 2.2% (3 of 138) of yearlings killed by hunters in Nevada and Utah had the udders removed was considered evidence that these animals had been lactating and, therefore, been bred as fawns (Robinette and Gashwiler, 1950). However, this evidence is circumstantial and not irrefutable. When this sample was extended to 540 yearlings, no more lactating animals were found (Robinette *et al.*, 1955). The finding of pigmented corpora lutea scars in 4.2% of yearling mule deer does (7 of 167) was taken by Robinette *et al.* (1955) as an indication that breeding may occasionally occur in fawns

Table II - Breeding in free-ranging white-tailed deer fawns

Percentage of female fawns breeding	Area	References
36% pregnant	Southern New York (good range conditions)	Cheatum and Morton, 1946
4.2% pregnant	Northern New York (poor range conditions)	
10.5% pregnant	Southern Ontario	Mansell, 1974
>41% pregnant	Southern Illinois	Roseberry and Klimstra, 1970 Follmann and Klimstra, 1969
26% conceived	S.W. Ozarks, Arkansas (poor range conditions)	Robb, 1959
74% conceived	Northern Missouri (good range conditions)	Robb, 1959
65% gave birth 74% conceived 82% ovulated	Iowa	Haugen, 1975
16% conceived	Llano Basin, Texas	Teer, Thomas and Walker, 1965

in the wild state. However, no pregnancies were found in 107 female fawns. As the udders were virginal in appearance and there is evidence (Golley, 1957) that in black-tailed deer corpora lutea of estrus occasionally form pigmented corpora albicantia, Robinette's et al. (1955) finding cannot be taken as evidence that these animals had bred. The same applies to Brown's (1961) finding of 2 pigmented spots usually characteristic of corpora albicantia derived from corpora lutea of pregnancy, in the ovaries of a black-tailed deer fawn collected in Washington in April. As there was no sign of an embryo, Brown surmised that this animal had bred but lost the embryos shortly after breeding which, in the light of Golley's (1957) findings, could be doubted. Neither can the finding of 1 corpus albicans in 1 of 99 15-17 month old mule deer by Anderson et al. (1970) be taken as certain evidence of pregnancy (Thomas, 1970).

Jensen and Robinette (1955) found a single nearly full-sized fetus in a 1 year old mule deer doe killed in an alfalfa field in Utah, and Nellis et al. (1976) reported that one 10-11 month old mule deer fawn (of a sample of 14) carried a 136 day old fetus (In both cases age was estimated by dentition). Thus there are only 2 irrefutable cases of reproduction in wild female mule deer fawns.

In the black-tailed deer there are only 3 authenticated cases of reproduction in free-ranging fawns. Shantz (1943) reported that in Oregon 2 black-tailed deer fawns were raised in partial captivity, released when 6 months old, and the next spring had doe fawns. These fawns in turn gave birth to doe fawns the following spring, although they had never been in captivity. They were, however, quite tame, indicating that they may have been receiving supplementary feed although Shantz does not say so. On November 16th, 1971 Thomas and Smith (1973) collected a female black-tailed deer on Vancouver Island. It was followed by 2 fawns and was lactating. The age was determined as 1 1/2 years by teeth eruption, wear pattern and histological examination of stained dental cementum. The ovaries contained 2 active and 2 regressed corpora lutea as well as 1 corpus albicans. This deer had obviously conceived as a fawn. According to Smith (pers. comm., 1975) it had been feeding mainly on farm crops.

Thomas (1970) found no sign of breeding in a total of 59 female black-tailed deer fawns, and no sign of having bred as fawns in 70 yearlings collected mainly in fall and winter from 1963 to 1967 at Northwest Bay, Vancouver Island. Also, no sign of breeding was found in 6 female fawns collected at Kelsey Bay, Vancouver Island, in January 1975 in the course of this study, or in 20 female fawns collected in fall and spring from 1968 to 1970 in McDonald Forest, Oregon (Jordan and Vohs, 1976). Each one of these collecting sites was in early stages of forest succession after logging and was, therefore, a good range as forage was of high quality and quantity (Bunnell and Eastman, 1976).

Normally, black-tailed deer reach puberty as yearlings, but some not until they are 2 1/2 years old (Brown, 1961). This delay was found to be linked to poor range conditions (Taber, 1953; Taber and Dasmann, 1957, 1958) -- in extreme cases even 2 year olds did not breed. According to Cowan (1956) many black-tailed deer yearlings on the poorer ranges of British Columbia do not breed.

It is, therefore, quite surprising to find in the literature several cases reported where captive or semi-captive black-tailed deer have reached puberty at less than 1 year of age, since conditions in captivity often are somewhat less than optimal (e.g. lack of space, high density, large parasite load). Cases of reproduction in captive or semi-captive female black-tailed deer fawns have been reported by Rampont (1926): a 15 months old doe in California gave birth to a single fawn, Shantz (1943): 2 approximately 1 year old does raised in partial captivity in Oregon each gave birth to 1 fawn, Cowan and Wood (1955): the mating of a fawn buck and a fawn doe at the deer unit of the University of British Columbia produced a viable offspring and Thomas and Smith (1973): 2 large corpora lutea in an unmated female aged 9 months at the U. B. C. deer unit. A semi-captive mule deer gave birth to a fawn at 13 months of age (Crane and Jones, 1953) and 3 captive female mule deer were bred when less than 8 months old (Robinette _et al_., 1973). A case of breeding in a captive male mule deer fawn was reported by Robinette and Gashwiler (1950: a captive 7 months old buck successfully bred a 19 months old doe in Utah). However, breeding in male fawns, contrary to that in female fawns, is not important in the breeding potential and the intrinsic population growth rate (Cole, 1954) of the species and has, therefore, not been included in this study.

It seems strange that a species would have, and maintain from generation to generation, the capacity to breed at an early age, but that this capacity would be realized so rarely within the extensive natural range of the species. This study, which was carried out from 1973 to 1976, attempted to shed light on this phenomenon by answering the following questions:

1. Does puberty at under 1 year of age in captive female black-tailed deer only occur in rare, exceptional cases of reproductively anomalous animals or does it occur regularly under certain conditions of captivity? Hediger (1964) stated that captivity caused sexual precocity in ibex and probably also in elephants and apes.

2. Is a nutritional factor responsible for precocious puberty? There is plentiful evidence in many species of deer, including O. h. columbianus, that nutrition influences the age at which puberty is attained (Cheatum and Severinghaus, 1950; Robinette et al., 1955; Brown, 1961; Klein, 1970.

3. If a nutritional factor is indeed responsible, would this be manifested in differential weights of breeding and non-breeding fawns?

MATERIALS AND METHODS

A. The Experimental Animals

All animals used in this study were Columbian black-tailed deer (*Odocoileus hemionus columbianus*). In the fall of 1972 an adult buck, a fawn buck and an unrelated adult doe were obtained from a captive herd on Vancouver Island to form the nucleus of a breeding herd. The adult buck was left untagged, the fawn buck was cryo-branded (Newsom and Sullivan, 1968) with the number 3, the doe was left untagged and given the number 0. In order to obtain a large number of fawns of known origin from one single population to start the main study, animals were subsequently collected from the wild. From June 1st to 20th, 1973, 17 newborn female fawns (plus 5 buck fawns) were collected in the Adam and Eve river valleys near Kelsey Bay on Vancouver Island. In addition 3 females and 3 males were obtained from people on other parts of Vancouver Island who had taken care of these fawns after they had been picked up as "abandoned". The Kelsey Bay fawns were captured by driving along logging roads and flushing does followed by fawns through conspicuous behaviour. The sudden flight of the dams caused the fawns to drop immediately (Cowan, 1956; Downing and McGinnes, 1969). On some occasions, when a doe was seen alone whose behaviour indicated that a fawn was hidden nearby, the fawn was located by imitating a fawn's distress call. Usually, the fawn's hiding place was revealed by the behaviour of the dam in response to this call (Linsdale and Tomich, 1953;

Mueller and Wooldrige, 1974 unpubl., Appendix A). The age of the fawns at the time of collection was estimated from their weight and general appearance to be between 1 day and 2 weeks. All animals were hand-raised. They were marked with yellow plastic ear-tags ("Lone Star", Y-TEX Corporation, Cody, Wyoming) bearing black numbers from 1 to 28, since marking by cryo-branding had proved to be unsatisfactory.

In 1974, between June 1st and 16th 10 female fawns (plus 1 buck fawn) were collected in the same area as the previous year, and 1 female fawn was obtained from the Fish and Wildlife Branch in Nanaimo. They were also estimated to be less than 2 weeks old. Two fawns refused to eat from the bottle and died within 1 week in spite of attempted force-feeding; the others were hand-raised. Four of these hand-raised fawns, after being marked with red "Lone Star" tags bearing white letters A, B, C, D, were released after weaning and thus were not available for studies on puberty. The buck fawn was killed by dogs. The 5 remaining females were marked E, F, I, J, K. In addition, in 1974 4 females and 3 males born in the research enclosure and raised by their mothers survived until the breeding season, and the females were used for studies on puberty attainment. They were also marked with red "Lone Star" tags bearing in white the dam's number and a letter, beginning with A for the first fawn: 5-A, 21-A, 22-A (females, born as singles to one-year-old dams), 0-B, (female, born as twin to adult dam), 11-A, 23-A (males, born as singles to one-year-old dams) and 0-A (male, born as twin to adult dam). For life histories and breeding records of experimental females see Appendix E.

In 1975 no more deer were collected in the wild, but 14 of the females born in the research enclosure survived at least until the breeding season. Six of them were hand-raised and 8 were raised by their mothers. All animals born in 1975 were marked with white "Lone Star" tags, bearing in black the mother's number and a letter. The female fawns which survived had been marked at birth as follows: 2-C, 3-C, 16-C, 17-B, 23-C (born as twins to 2 year old dams, hand raised), I-B (born as twin to 1 year old dam, hand-raised), 5-C, 16-B, 17-C, 22-C (born as twins to 2 year old dams, mother-raised) O-D (born as twin to adult dam, mother-raised), and 18-A, 19-A, 31-A (born as singles to 2 year old dams, mother-raised). In addition, several males were born and several female fawns died in 1975 (as in 1974) from various causes (coccidiosis, lactation failure of the mother, attack by dogs) before the fall.

Certain fawns born in the research enclosure in 1976 were marked in the same way as the ones born in 1975 (white tags, black lettering) and some of these 1976 fawns were also used to obtain more data on early weight development and the attainment of puberty. Only 3 of the hand-raised animals were extremely tame (1973: #6, #27; 1974: #K) and could be handled with relative ease — presumably because they had been raised for some time alone before joining the fawn herd (collected by hikers etc., later donated to the project) — while the others became timid after being weaned and would not let themselves be touched, although they were not alarmed by the presence of humans. The mother-raised animals were much shyer, and their flight-distance was somewhere between that of hand-raised and that of wild deer.

The dams of the fawns collected in the wild were considered to be in good physical condition at the time of parturition. This can be attributed to the abundance of food available to them since both the Adam and Eve river valleys were in early stages of succession after being almost totally cleared of mature stands of timber by logging, thus providing optimal browse conditions (Bunnell and Eastman, 1976). Nothing is known about the state of nutrition of the dams of the fawns who were initially cared for by other people. The physical condition of the does giving birth in the enclosure was comparable to that observed in wild does.

B. Facilities for Maintenance and Manipulation of Experimental Animals

On June 20th, 1973 the fawns were transferred by truck from the capture area to an open-sided greenhouse in West Vancouver (16.5m x 4m) which had been temporarily converted into a deer enclosure by covering the sides with chain-link wire. The floor consisted of earth. The fawns were kept there in a group for hand-raising until October.

In 1974, after being brought in from the capture area on June 16th, the fawns were kept for hand-raising at a similar facility: a 5 x 10m chain-link enclosure with a polyvinyl roof and earth floor. In 1975 (after removal from their captive dams at about 3 days of age) fawns were kept in a 5 x 5m enclosure without a roof but with access to a covered shed. In each of the

3 years the fawns were weaned on October 1st and transferred from the raising facility to the research enclosure on the same date.

The research enclosure (Figure 1) was a fenced off area of the U. B. C. Research Forest in Maple Ridge, B. C., measuring 137m x 78m (approx. 1 hectare). It consisted of a low lying part (2/3 of area) with a permanent and a seasonal creek running through it, and a rocky bluff (1/3 of area). The rocky section was covered with 10 year old conifers — Douglas Fir [Pseudotsuga menziesii, (Mirb.) Franco], Western Hemlock [Tsuga heterophylla, (Ref.) Sarg.], Western Red Cedar (Thuja plicata, Donn.) mixed with a few Red Alders (Alnus rubra, Bong.), and the low lying part, which was quite swampy except during the summer, with rushed (Juncus sp.). The trees and a shingle-roofed shed (7m x 2.5m) provided the only shelter from the weather. The fence was 3.5m high -- the lower part (1.2m) consisting of chain-link wire of which about 20 cm were dug into the ground, and the upper part of spot-welded wire mesh. Feed was given in a hay rack and a wooden feed trough (both 5m long) which were covered by a roof. If the size of the herd made it necessary, additional feed troughs were also put out under the shelter.

In the northwest corner of the research enclosure a special structure was built for animals which had to be frequently handled or kept separately (Figure 2a). It consisted of a circular, wooden building covered by a cone-shaped roof and contained 20 individual stalls, all opening with a door to the centre from where they could be serviced and to the outside into wedge-shaped,

Figure 1 - One hectare research enclosure at U. B. C. Research Forest, Maple Ridge, British Columbia.

(not to scale)

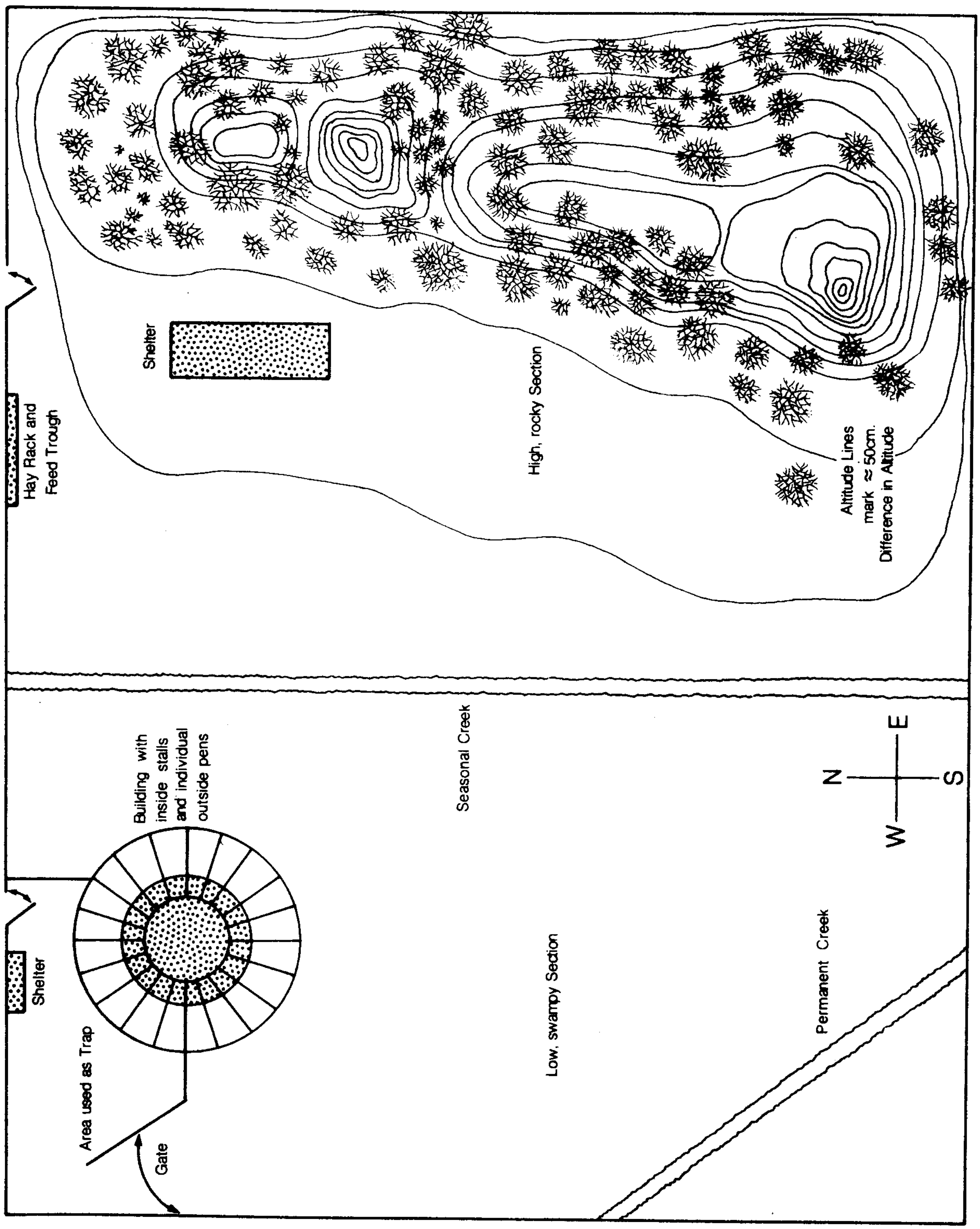
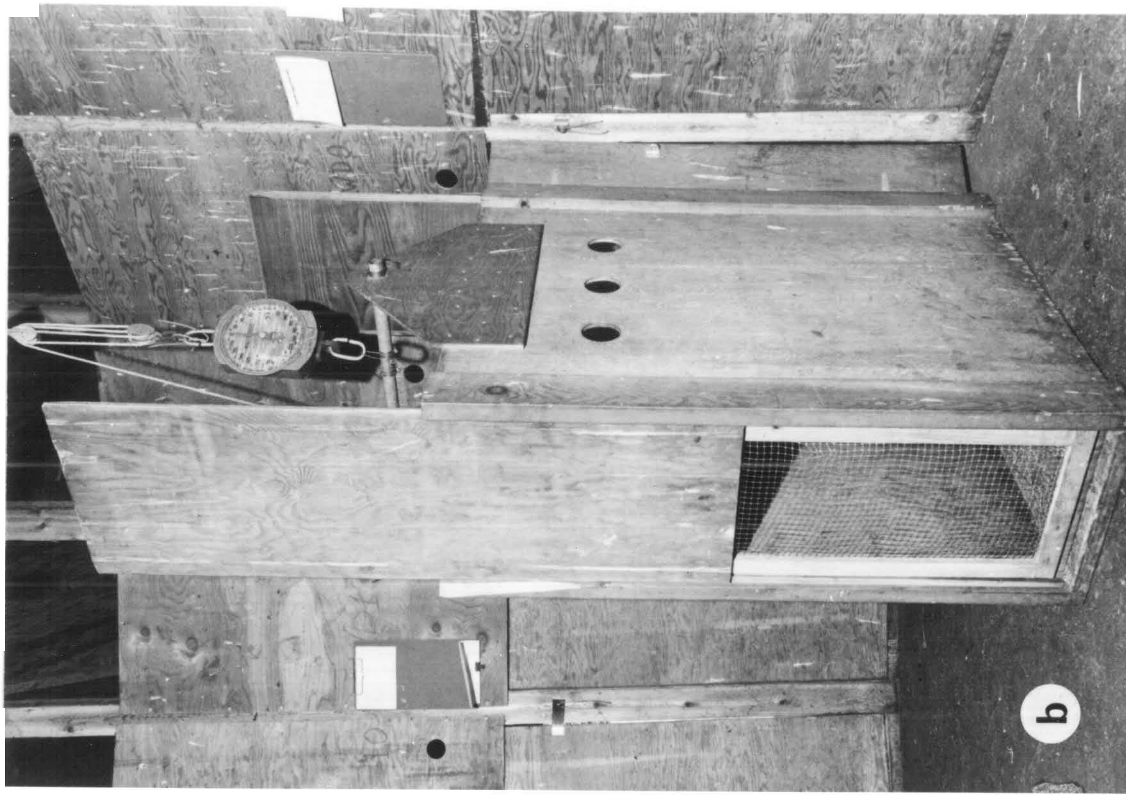

Gate
Hay Rack and
Feed Trough
Shelter
High, rocky Section
Altitude Lines
mark ≈ 50cm.
Difference in Altitude
Seasonal Creek
Gate
Shelter
Building with
inside stalls
and individual
outside pens
Area used as Trap
Gate
Low, swampy Section
Permanent Creek
N
E
S
W

Figure 2 - a. Circular building with stalls and outside pens used to keep deer individually.

b. Weighing box and spring scale used to weigh experimental deer.


b


a

2.44m high chain-link wire pens. The floor of the building and the pens was made from asphalt. The dimensions of this structure were as follows: The central area of the building was 4m in diameter and 4.45m high in the centre. Each stall was 2.3m long, 65cm wide at the inside and 105cm at the outside, the adjacent outside pens were 7.08m long and 3.46m wide at the outside. Feed was provided in the stalls in wooden troughs, water in plastic containers. By connecting the fence surrounding this structure to the perimeter fence of the main research enclosure a corner was fenced off which could be used as a trap if certain animals had to be caught, or as an additional, separate holding pen. It also had a small shelter (3.5m x 1.2m).

C. Feeding Regime for Hand-raising of Fawns

Since it is not possible to obtain deer milk in large enough quantities to feed it to fawns which are being hand-raised, a substitute formula must be used. For economic and practical reasons it is best based on cow's milk or products made from it which are always available at reasonable cost.

There is a great difference in composition between cow's milk and milk of black-tailed deer (Tables III, IV, and Appendix C). Kitts *et al.* (1956) suggested modifying cow's milk by a) diluting it with water to lower the lactose content and b) adding fat (vegetable oil) and protein (casein) in order to approximate the properties of doe's milk as closely as possible. In spite of the great difference in composition between evaporated milk and milk of black-tailed deer (especially with regard

Table III - Comparison of nutrients in deer and cattle milk

Species	# of does	# of samples	Particulars		Nutrients as % of whole milk Fat	Protein	Lactose	References
Black-t. Deer (O.h.columb.)	1	1	Dead animal in early stages of lactation (June 10)		8.3			Hagen (1951)
Black-t. Deer	2	1	3 year old doe alive, 28th day of lactation		10.5	9.56	3.91	Kitts et al. (1956)
		1	Same animal, dead 28th day of lactation		10.5	8.96	4.67	
		1	Terminal stage of lactation		10.2	8.14	4.55	
Black-t. Deer	3	10 *	1 year old entire lactation	x̄	15.29	6.75	3.59	This study **
				max.	21.2	10.2	6.96	
				min.	9.62	6.76	1.6	
		12 *	2 year old entire lactation	x̄	14.04	8.7	3.74	
				max.	15.4	11.12	6.81	
				min.	11.23	6.66	2.13	
		18 *	Adult, first 34 weeks of lactation	x̄	14.26	8.76	3.35	
				max.	17.8	11.9	5.27	
				min.	10.26	6.73	2.08	
Mule Deer (O.h. hemionus)	3	1	About 2 year old dead early lactation (July)		8.13			Browman and Sears (1955)
		1	2 1/2 year old, dead, middle of lactation (August)		8.4			
		1	2 1/2 year old, dead, beyond middle of lactation (September)		13.6			
White-t. Deer (O. virginianus)	1	1	1 year old, 3rd week of lactation		7.3	7.04	4.28	Murphy (1960)
White-t. Deer	2	1	Dead, last stage of lactation (November)		18.00	11.50	2.22	Silver (1961)
		1	Prob. colostrum		8.00	8.83	3.82	
		1	End of 1st week		8.00	10.65	2.85	
		1	End of 1st month		7.50	10.14	3.00	
		1	End of lact. (5 mos.)		11.50	18.00	2.22	
White-t. Deer		34	1 to 21 days of lact. (Not milked empty)	x̄	9.5			Youatt, Verme and Ullrey (1965)
				max.	10.3			
				min.	8.1			
Domestic Cow		General			4.4	3.8	4.9	Espe and Smith (1952)
		General			4.5	3.77	4.86	Wright et al. (1939)
		General			3.65	3.13	4.5	
		Mean			3.8	3.55	4.9	Petersen (1950)
Domestic Cow, evaporated		General			7.8	6.8	9.6	Pers. Comm., Carnation Co. Ltd. (1975)
		General			7.8	6.5	9.5	Petersen (1950)

* Each sample consisting of 2 - 4 subsamples, representing 1 - 2 weeks of lactation
** Percentages of nutrients derived by analyses according to Appendix C

Table IV - The caloric value of milk (kcal/kg)

Species	Ear Tag #	Type of milk	Average caloric content (kcal/kg)		References
Black-t. deer		3 single samples	1650		Kitts *et al.* (1956)
	0	$\bar{x}$ first 34 weeks (n=18) of lactation	1768 (1)	1945 (2)	This study (see App. C)
	10	$\bar{x}$ entire lactation (n=14)	1761 (1)	1937 (2)	This study (see App. C)
	1	$\bar{x}$ entire lactation (n=13)	1790 (1)	1931 (2)	This study (see App. C)
Domestic cow		fat corrected	750		Kitts *et al.* (1956)
		3.4% fat	693		Dairyland Co. (pers. comm.)
		evaporated milk	1440		Dairyland Co. (pers. comm.)

(1) calculated: $E = 9F + 4P + 4L$ (2) calculated: $E = 9.11F + 5.86P + 3.95L$ (Perrin, 1958)

F, P, L: g/kg, determined by analyses according to Appendix C.

F: Fat
P: Protein
L: Lactose

to fat and lactose) the difference in caloric value is not very great (Table IV) as fat and lactose in evaporated cow's milk and deer's milk largely offset each other.

In 1954 one of Kitts' co-workers (Bandy, 1955) had tried to raise black-tailed deer fawns on evaporated milk diluted with water and, when the animals developed digestive difficulties which he attributed to dilution, changed this to concentrated evaporated milk with corn oil on which he raised 7 fawns successfully. His conclusion, however, although in agreement with Silver's (1961) suggestion that digestive disturbances (in white-tailed deer fawns) may result from too dilute formulas, contrasts with that of Pinter (1962) who surmised that diarrhea in hand-raised fawns was caused by the high lactose content of cow's milk and, therefore, diluted it with water to feed roe deer (Capreoleus capreolus) fawns. The formula suggested by Kitts et al. (1956) was improved by Murphy (1960) by adding vitamins, minerals, trace elements and emulsifier and was used to successfully rear 6 white-tailed deer fawns in 1958. However, when Bandy in 1956 again raised a large number (66) of black-tailed deer (Bandy, 1965) he did not follow the suggestions of Kitts et al. (1956) but fed his animals undiluted evaporated milk fortified with minerals and trace elements, which was only diluted to 50% with water for feeding the fawns shortly after capture. Forty of these fawns contracted scours and 10 of them died.

It appears that almost everyone who has raised deer fawns used a different formula and considered it to be optimal. Müller-Schwarze (1969) raised black-tailed deer fawns on straight goat's milk. Trainer (1962) reported that of 435 white-tailed deer fawns 387 (89%) were successfully reared on raw whole cow's milk which, for the first 2 weeks, was diluted to 50% with water and then gradually changed until, from 4-5 weeks of age, the fawns received straight cow's milk. Wagner and Cociu (1967) obtained positive results by hand-rearing a variety of mammalian species, including roe deer, on reconstituted dry milk which contained 10% dry milk for the first few days, and 20% thereafter. Youngson (1970) reported 11 red deer calves having been successfully raised on full-cream milk powder reconstituted to approximate the composition of cow's milk. Silver (1961), who experimentally compared white-tailed deer fawns raised on evaporated milk, whole cow's milk and by their own mothers, found those raised on evaporated milk to develop faster than the mother-raised animals and with less digestive upsets than the ones raised on whole cow's milk. Long _et al_. (1961) also experimentally compared white-tailed deer fawns raised on different diets and found that feeding with raw milk resulted in the greatest gains while evaporated milk was second, pasteurized homogenized milk third and synthetic milk replacer last. Wood _et al_. (1961) found evaporated milk, for the first 4 weeks diluted with water decreasingly from 50% to 0%, a completely satisfactory diet for black-tailed deer fawns when supplemented with trace elements.

Based on these and previous personal experiences and for reasons of practicality, the decision was made to feed all the fawns which had to be hand-raised in the course of this study on evaporated milk which was diluted with water only during an initial period (Table V).

Table V - Formulae used in hand-raising of fawns

Year	Time Period	Composition of Formula
1973	From capture - June 29	: 1/2 evap. milk, 1/2 water
	June 30 - July 22	: 2/3 evap. milk, 1/3 water
	July 23 - Sept. 30	: undiluted evap. milk
1974	From capture - June 16	: 1/2 evap. milk, 1/2 water
	June 17 - July 7	: 2/3 evap. milk, 1/3 water
	July 8 - Sept. 30	: undiluted evap. milk
1975	From 2-3 days after birth - approx. 10 days after birth	: 1/2 evap. milk, 1/2 water
	From approx. 11 days after birth - Sept. 30	: undiluted evap. milk

These formulae were heated to 40°C and fed from soft-drink bottles on which a cc graduation was painted and which were fitted with lambs nipples.

The bottles were thoroughly cleaned after each feeding but not sterilized.

In each of the 3 years when fawns were hand-raised, they were fed by not more than 2 persons who remained the same throughout the nursing period. They were fed to satiation 4 times a day (at 0900, 1400, 1900, 2400). This feeding schedule was based on personal experiences in hand-raising of ungulates. It approximated nursing by the dam as shown by observations made on 3 nursing does in the course of this study in 1975: During the initial stages of nursing there were 5 to 6 suckling periods per day which, at the 6th to 8th week, were reduced to 3 suckling periods. For the first 2 weeks the anal and perianal region of the fawns was gently massaged with toilet paper during nursing to ensure regular defecation and urination and to stimulate suckling (Müller - Schwarze, 1969).

To wean the fawns, the number of feedings in 1973 was reduced to 3 feedings on September 4th, 2 feedings on September 7th and 1 feeding on September 15th. In 1974 4 feedings were maintained throughout, but during the last 3 days the quantity of milk was reduced to 160cc per feeding (from an *ad libitum* intake of approximately 300-400cc). In 1975 the number of feedings was reduced to 2 on September 21st and to 1 on September 27th. The fawns were weaned without difficulties and with no change in their growth rates. From October 1st on the fawns were given no more milk.

The date for weaning was set arbitrarily as there is little definitive information on the natural time of weaning in the species *O. hemionus*. Some observers have stated that weaning takes place at approximately 2 to 2 1/2 months of age (mule deer:

Dixon, 1934; Clark, 1953; black-tailed deer: Taber and Dasmann, 1958). Linsdale and Tomich (1953) noted that most black-tailed deer fawns in California are weaned in September while in British Columbia lactating does can still be found in November (Thomas and Smith, 1973). In the present study a 1 1/2 year old and a 2 1/2 year old doe ceased lactating at the beginning of December, while an adult doe of unknown age was still lactating in January.

Pelleted cattle feed (see "Feeding after Weaning"), alfalfa hay and fresh browse [Salmonberry (*Rubus spectabilis*, Pursh), Willow (*Salix* sp.) Vine Maple (*Acer circinatum*, Pursh) Broad-leafed Maple (*Acer macrophyllum*, Pursh)] as well as water were available *ad libitum* and, starting from about 1 week of age, the fawns ate increasingly larger quantities of solids. During the first month all fawns twice received 1cc Pro-Vite (Vit. A, D, E,; Ayerst Lab., Montreal, Quebec) mixed with their formula.

Sixteen individual fawns in 1973 were observed to begin ruminating between July 14th and August 18th, with a mean date of July 27th and a mean age of 50 days (36-73). The age of these fawns was estimated *a posteriori* by regression formula 1, Table X. This observation indicates that solid food is important to the nutrition of fawns at a very early age.

All fawns also ate earth and feces. This coprophagia facilitated an outbreak of bacterial scours (Coli enteritis) in 1973 which affected almost all fawns, after a scouring mule deer fawn had been introduced into the herd (Table VI). No bacterial scours occurred in 1974, but in 1975 again several fawns were affected.

Bacterial scours are common in fawns that are being hand-

Table VI - Incidence of coccidial and bacterial enteritis in fawns and resultant mortality

Coccidiosis in mother raised fawns

	Sample size	Contracted disease	Succumbed to disease	Cured
1974	14	7	3	4
1975	29	3	2	1
1976	27	8	3	5
Total	70	18	8	10

Bacterial scours in hand-raised fawns

	Sample size	Contracted disease	Succumbed to disease	Cured
1973	31	23	0	23
1974	10	0	0	0
1975	6	6	0	6
Total	47	29	0	29

raised and often result in the death of the animals (Bandy, 1965; Long *et al*., 1961). Contrary to the belief of some workers that this digestive disturbance is caused by the milk formula being too diluted (Bandy, 1955; Silver, 1961) or not sufficiently diluted (Pinter, 1962), there can be no doubt that it is a bacterial illness caused by *Escherichia coli* with diet only playing a predisposing role (Kramer *et al*., 1971; Manninger and Mocsy, 1959). It responds promptly to antibiotic therapy (Trainer, 1962; Wagner and Cociu, 1967) which, in this study, was supplemented by dietary measures. As soon as diarrhea in a fawn was discovered, the animal was no longer fed milk. Instead, at the regular feeding times, it received camomile tea *ad libitum*, which has healing properties and replaces the fluid which is lost due to diarrhea. Once a day 1cc Chloralean (1cc = 150 mg Chloramphenicol; MTC Pharmaceuticals Ltd., Hamilton, Ontario) was mixed with the tea, which was always taken by the fawns without hesitation. Usually, the diarrhea disappeared within 1 day of treatment. The day following the illness the convalescent animal was given its milk formula mixed with some Kaopectate (kaolin plus pectin; Upjohn Co. of Canada, Don Mills, Ont.) and flax-seed mucus. With this treatment all fawns which had contracted bacterial scours recovered without exception (Table VI), and weight losses or reductions in the growth rate due to prolonged illness did not occur.

None of the fawns raised by their mothers developed bacterial scours. This can probably be attributed to the ingestion of antibodies with the mother's milk. However, a considerable proportion of these mother-raised fawns contracted coccidiosis (Table VI) which was diagnosed by coprological examination (oocysts of Eimeria sp.). This disease developed in the late stages of nursing when the fawns were already eating appreciable quantities of solids. If coccidiosis was diagnosed in its early stages, it usually responded to treatment with Polyansyn (effective ingredient: Sulfamethacine; Ayerst Lab., Montreal): 20cc/day given per os for a period of 3 to 4 days until diarrhea stopped.

D. Feeding after Weaning

Work on laboratory and farm animals has shown that puberty in female mammals is affected by the level of nutrition and that an insufficient supply of protein can delay puberty very significantly, even when the total amount of food eaten is normal (Perry, 1971). Furthermore, many researchers have especially emphasized the importance of protein to the growth, health and reproduction of deer (Einarsen, 1946; French et al., 1956; Taber and Dasmann, 1958, Swank, 1958, Daniel, 1963; Murphy and Coates 1966, Ullrey et al., 1971; Robinette et al., 1973).

Diets devised to be optimal for the maintenance and propagation of deer in captivity have, therefore, always been formulated to contain a high percentage of protein. Bandy (1955) used the formula shown in Table VII (U. B. C. ration #15-52) to feed black-tailed deer at 2 quantitative levels without other nutritive supplements. He used an almost identical formula (U. B. C. ration #15-56) in 1957 (Bandy, 1965). A similar ration was formulated

Table VII - Feed formulae on which black-tailed deer were successfully maintained

A. U.B.C. Deer Ration #15-52, base components

	% of wet weight	% of dry weight
Moisture	10.4	
Protein	15.4	17.3
Fat	4.0	4.5
Fibre	8.4	9.5
N.F.E.	53.6	60.0
Ash	7.7	8.7

B. Buckerfield 20% Calf Starter Pellets, formulation in lbs./metric ton

				Compl. Horse Micro Mix:				
Crushed Barley	625	Rapeseed Meal	90	Vit. A mil. i.u.	10	Choline Chloride	gm	100
Crushed Oats	100	Soybean Oil	20	D mil. i.u.	2	Copper	gm	6
Crushed Corn	200	Alfalfa Dehyd.	60	E thous. i.u.	20	Manganese	gm	50
Bran	110	Salt	15	K gms	1	Zinc	gm	60
Shorts	140	Phosph. Defl.	10	B12 mg	2.9	Iron	gm	10
Soybean 48 1/2%	375	Limestone	10	Riboflavin gm	1.33	Cobalt	gm	2
Malt Sprouts	75	Molasses	165	Niacin gm	12	Iodine	gm	2
		Compl. Horse Micro Mix	5	Cal. Pantothenate gm	8.1	Penicillin	gm	2
				Folic Acid gm	0.5			

C. Simon Fraser University Experimental Deer Ration: 3 isocaloric formulae, differing in protein, formulation in lbs./metric ton

	15% Protein	10% Protein		7 % Protein
Ground Barley	700	570		820
Ground Oats	300	750		
Ground Corn	150	500		500
Shorts	400		Cassava Meal	500
Soybean 48 1/2%	125			
Malt Sprouts	100			
Alfalfa Dehyd.	30			
Salt	10	20		20
Phosph. Defl.	5	5		5
Limestone	25	25		25
Dist. Sols.	50			
Molasses	100	125		125
Compl. Horse Micro Mix	5	5	Dairy Micro Mix (see below)	5
Total	2000	2000		2000

Dairy Micro Mix		
	Mit. A. mil. i.u.	12.5
	D 3 mil. i.u.	6.8
	E. thous. i.u.	6.
	Copper gm	12.8
	Manganese gm	30.
	Zinc gm	176.
	Cobalt gm	3.8
	Iodine gm	9.35
	Magnesium gm	180.

by Ullrey *et al*. (1971) for white-tailed deer. In this study the following pelleted feeds were used:

A. Calf Starter Pellets (Buckerfield Ltd., Vancouver, B. C.), containing 20% protein (min.), 4% fat (min.) and 6.7% fiber (Table VII). Digestible energy was 3167 kcal/kg.

B. Full-Flow Dairy Pellets (Buckerfield Ltd.)

1. containing 16% protein (min.), 3% fat (min.) and 7.7% fiber. Digestible energy was 3140 kcal/kg.
2. containing 14% protein (min.), 3% fat (min.) and 9% fiber (max.).

The formulation of these feeds was not available from the manufacturer.

C. Simon Fraser University Experimental Deer Ration: 3 isocaloric formulae, differing in protein (Table VII).

As previously mentioned, all fawns used in this study had free access to solid food (pelleted feed, alfalfa hay and fresh browse) during the nursing period. After weaning (October 1st) the same foodstuffs were fed *ad libitum*, although browse was discontinued during the time when the deciduous trees were without leaves. This diet was supplemented with some pen vegetation which was only of substantial quantity in early fall of 1973, but soon decreased to an insignificant amount thereafter because the deer destroyed almost all palatable vegetation within reach.

Alfalfa hay was available *ad libitum* throughout the study to all deer except those on a reduced protein diet. Deer do not eat the coarser parts of alfalfa hay, and in order to reduce waste only 3rd and 4th cut, containing a higher proportion of the leaves and fine stems which alone are taken by the deer, was fed. The portion of the alfalfa hay which is actually ingested contains 18.7% of protein (Smith, 1952).

E. Weights and Measurements

Three measurements of body size were taken and recorded at intervals in order to assess the growth of the experimental animals: weight (in kg), length of hind-foot and heart girth (in cm). Heart girth is the minimal chest circumference at the height of exhalation directly caudal of the scapulae. The length of the hind-foot is the distance from the point of the hoof to the tip of the calcaneus. The measurements were taken with a plastic measuring tape.

A third commonly used linear measurement, namely height of withers (Bandy, 1955; Brody, 1964) was omitted. The accuracy of this measurement was unsatisfactory due to the nervousness and constant movements of the deer and their tendency to lower their pectoral girdle when touched at the withers. The weighing and measuring schedule is outlined in Table VIII.

Young fawns were weighed by a person holding them while standing on a platform scale with a maximum capacity of 160 kg. and a 0.1 kg. graduation (Health-O-Meter, Continental Scale Corp., Chicago, Ill.). The fawns were usually too heavy for this procedure after October, and from then on they were weighed in a wooden box (length: 91cm, height: 122cm, width: 41cm). This box had vertically sliding solid doors at both ends and, in addition, on one end a wire-screen door (Figure 2b). To place an

Table VIII - Weighing and measuring schedule

Year's Class	Mode of Rearing	Time Period	Weighing Schedule	Measuring Schedule
1973	hand r.	Capture-end of Jan.	once a week	once a week
		end of Jan. →	irregularly	
1974	hand r.	Capture-end of Sept.	once a week	once a week
		end of Sept.-Mid. of Jan.	once a week	
		middle of Jan. →	irregularly	
1974	mother r.	Birth-mid. of Sept.	daily	
		mid. of Sept. →	irregularly	
1975	mother r.	Birth-end of June	daily	irregularly
		Beg. of July - end of Aug.	once a week	once a week
		end of Aug.-beg. of Oct.	once a week	
		Beg. of Oct. →	irregularly	
1976	mother r.	Birth - end of July	daily	
		end of July →	irregularly	

animal into the box both solid doors were lifted up, and the open end of the box was placed in front of the opened door of a stall. The fawns were then driven into the box and trapped when the solid sliding doors were dropped. The box was connected by a spring-scale with a maximum capacity of 400 lbs. and a 1 lb. graduation (No. 118 Detecto Matic, Detecto Scales, Inc., Brooklyn, N. Y.) and a rope and pulley to a steel beam which projected at right angle from the vertical, wooden centre pillar of the circular building at the research enclosure. This steel beam could be moved in a circular fashion with the wooden pillar as a hub. By using the pulley, the box could be easily lifted by one person for weighing or for moving it from one stall to the next. As far as possible the animals were weighed at the same time of day at each weighing. Mother-raised fawns while nursing and weaned fawns were weighed in the early afternoon, which is a time of reduced activity for the deer and is about halfway between the morning and evening feeding periods. Nursing hand-raised fawns were weighed before the morning feeding.

As deer grow larger and less manageable it becomes more difficult to restrain them in order to take accurate linear measurements. Therefore, after few months of age linear measurements were only taken in a few cases. Additionally, weight is the fastest changing parameter as it is only 6% of the adult weight at birth, while heart girth at birth is 27% of this measurement in adults, and hind-foot length is 45% (Bandy, 1955). Changes in body size and differences of growth with time between individual animals are, therefore, most readily detectable in series of weight measurements (Figure 3).

In order to document the variation in growth curves and to compare growth between different groups of animals, it is necessary to describe the growth pattern mathematically (the object of this description was to compare individuals and groups of deer prior to and at puberty and not to derive growth rates or growth constants). Four types of comparisons were formed:

1. Linear regression and curvi-linear regression formulae to the point of inflection (self-accelerating phase*)
2. Weights achieved at specific ages.
3. Time to double birth weight.
4. Weight at breeding season as percentage of adult weight.

F. Age Estimation of Wild-Caught Fawns

After the female fawns that were to be used in this study had been collected in the wild, the problem of determining their age presented itself. They were almost certainly not older than 2 weeks (but probably much younger) at the time of capture, since black-tailed deer fawns only respond to danger by "dropping" behaviour for a very short time after birth (Cowan, 1956) and, therefore, can be collected by simply picking them up only on rare occasions after the 3rd week of June (Thomas, 1970; Brown, 1961). At this time the oldest fawns are about 3 weeks old. For this study no fawns were collected after June 20th in 1973 and June 15th in 1974.

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*This phase of growth was described by Brody (1964) as being characterized by "the principle of compound interest, with the interest added to the capital from moment to moment" (p. 515).

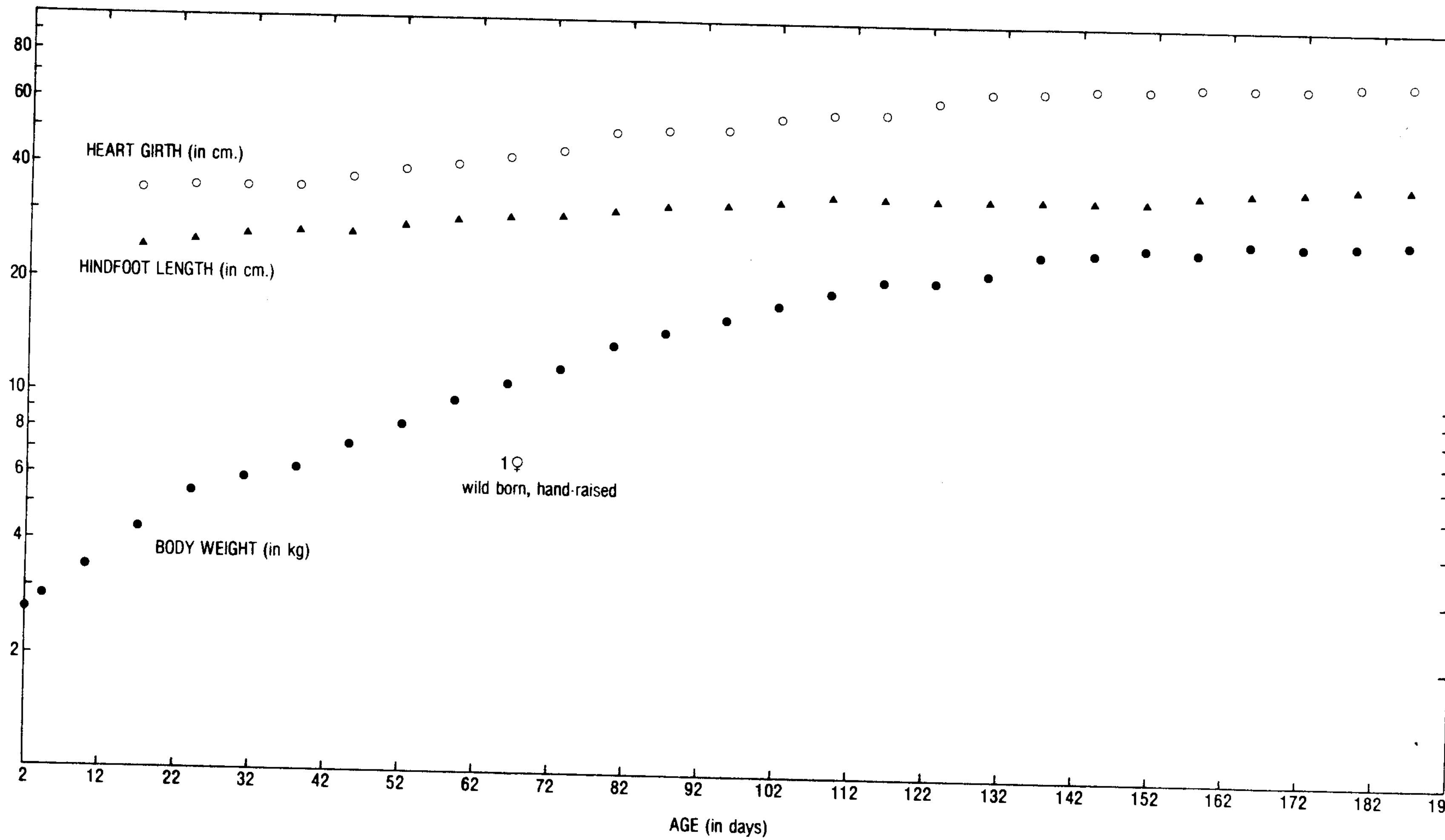
Figure 3 - Typical growth curves (female #1, wild born hand-raised).

Capture date: June 8, 1973

Estimated age at capture - if singleton: 0 days

- if twin: 2 days

Fig. 3


HEART GIRTH (in cm.)
HINDFOOT LENGTH (in cm.)
BODY WEIGHT (in kg)
1♀
wild born, hand-raised
AGE (in days)
80
60
40
20
10
8
6
4
2
2
12
22
32
42
52
62
72
82
92
102
112
122
132
142
152
162
172
182
192

The reason for estimating the age at capture and thus the date of birth was to record as accurately as possible age and size of these deer at the time of their first conception. This date was determined by subtracting 203 days from the date one day before parturition. However, 203 days represent the mean of the gestation period (Golley, 1957: 199-207 days, $\bar{x}$ = 203, n=5) which can range from a minimum of 183 days to a maximum of 212 days (Cowan, 1956; n=10). An error of up to +20 or -9 days in calculating the conception date by using the mean of the gestation period is therefore possible. In order to minimize a second source of inaccuracy when calculating the age of a wild-caught deer at conception, its birth date was estimated more accurately by a regression formula.

For the calculation of this formula (and 3 other formulae which later were not used for age estimation) data were only used from animals that a) were of the same stock as the fawns whose age was to be estimated (Kelsey Bay stock), b) were of the same sex, c) had been measured daily for the period from which the data were used, and d) had not suffered from any long-term illness. This formula was developed from the daily measurements of body weight for the first 9 days post partum of 7 mother-raised twin female fawns born at known times in the experimental herd in 1975 (Table IX). The data of twins were chosen, because Thomas' studies at N. W. Bay (an area similar and close to the collection site of the experimental deer) showed that 100 does produced 137 fawns, which means (as almost 100% became pregnant) that there are slightly more twins than singletons (74 twins to 63 singletons)

Table IX - Age estimation formulae for female fawns

	# of individuals	data points	age range	formula	r
1. 1975 data (twins)	7	63	Birth - 9 days	<u>y=2.29+0.168x</u>	<u>.716</u>
2. 1974 data (singletons)	6	48	Birth - 9 days	y=2.70+0.210x	.863
3. 1975/76 data (twins)	14	202	Birth - 15 days	y=2.50+0.147x	.754
4. 1974/75/76 data (singletons)	9	86	Birth - 15 days	y=2.66+0.192x	.895

y = wt (kg)   x = age (in days)

Underlined formula was used to estimate age of captured wild fawns.

born and that, therefore, presumably a larger percentage of the collected fawns were also twins (Thomas, 1970). The fact that a fawn was caught as a singleton or a twin did not necessarily mean that it had been born as such. Its sibling could have died, been killed by a predator or not been detected during the capture operation. It was also found that, if another regression formula was used which was developed from the weight data for the first 9 days post partum of 6 single fawns born in captivity in 1974 (Table IX), the age of captured wild fawns calculated from their weight by this formula differed only by a maximum of 4.6 days (singletons grow faster than twins) from that determined by using the data of 7 twins born in 1975 (Table X). The use of the twin formula for all fawns was, therefore, considered to be justified.

In 1976 more data on fawn growth were obtained and the regression formulae were revised (Table IX). The difference in the estimated ages of captured wild fawns by using the 1975 data or the combined 1975/76 data were so small, that the use of the original formula (formula 1, Table IX) was continued. It should be pointed out that an inaccuracy of a few days in estimating age is negligible when comparing does who did or did not attain puberty. Growth in late fall is extremely slow and weight changes little in a few days.

Table X shows the weights of the fawns at capture and their ages calculated from these weights by the 4 different regression formulae (Table IX). Animals who were not collected by the author, and whose weight at capture and development following

Table X - Estimates of ages at time of capture

Tag #	Caught as Twin or Singleton*	Capture date	Weight at Capture (in kg)	Estimated age at capture (In days) (based on numbered formulae of Table IX) if twin		if singleton	
		1973		1.	3.	2.	4.
1	S	8-6	2.6	1.8	0.7	0	0
2	S	10-6	4.0	10.2	10.2	6.2	6.9
3	S	10-6	3.3	6.0	5.4	2.8	3.3
8	S	14-6	2.7	2.4	1.4	0	0.2
10	T	15-6	3.7	8.4	8.2		
11	S	15-6	4.4	12.6	12.9	8.0	9.0
12	S	15-6	3.3	6.0	5.4	2.8	3.3
14	T	15-6	3.2	5.4	4.8		
15	S	16-6	4.3	12.0	12.2	7.6	8.5
16	S	16-6	2.6	1.8	0.7	0	0
17	S	16-6	2.5	1.3	0	0	0
18	S	17-6	4.4	12.6	12.9	8.0	9.0
19	S	17-6	2.3	0	0	0	0
21	S	18-6	3.4	6.6	6.1	3.3	3.8
22	T	19-6	4.5	13.1	13.6		
23	S	19-6	3.7	8.4	8.2	4.8	5.4
24	S	20-6	4.3	12.0	12.2	7.6	8.5
		1974					
A	S	7-6	3.2	5.1	4.8	2.4	2.8
B	S	7-6	2.75	2.7	1.7	0	0.4
C	S	9-6	2.8	3.0	3.4	0	0.7
D	T	12-6	2.75	2.7	1.7		
E	S	13-6	2.05	0	0	0	0
F	T	14-6	3.65	8.1	7.8	4.5	5.1
G	S	14-6	3.25	5.7	5.1	2.6	3.0
I	T	15-6	4.15	11.1	11.2		
J	T	15-6	2.55	1.5	0.3		

* If fawn was caught as singleton it could have been born as singleton or twin

capture were therefore unknown, were omitted in order to avoid errors in age calculation.

G. Experimental Arrangements

On October 1st, 1973 23 female black-tailed deer which had been hand-raised were taken to the research facilities at the U. B. C. Research Forest and 14 of them were used in an experiment investigating the influence of weight on the attainment of precocious puberty. It was attempted to produce a lesser weight gain through quantitative reduction of feed intake in an experimental group. While a control group of the 7 heaviest fawns was maintained on *ad libitum* intake, the intake of the experimental group of the 7 lightest fawns was restricted to 70% (of *ad libitum* intake during last week before start of experiment) for a 48 day period (Table XI). Only the lightest fawns were used in the experimental group so that, if the low plane of nutrition was to produce a decrease in the rate of weight gain, this would increase the already existing weight difference between the animals in the experimental group and in the control group. If no decrease in weight gain was produced by this experiment (which was expected as weight increases after the inflection point are minimal even at *ad libitum* diets) there would still be 2 groups with significantly different mean weights. If weight is a determining factor in the attainment of puberty one would expect a significant difference in the number of precocious breeders between the 2 groups. The percent weight increase rather than the instantaneous relative growth rate was chosen for comparison, because in some

Table XI - Regime for feed quantity reduction experiment 1973

Prior to October 1:	All fawns on evaporated milk (+20% protein pellets + alfalfa). *Ad libitum* intake.	
October 1:	14 fawn does placed in individual pens. Divided into two groups:	
	Group 1 (7 lightest fawns)	Group 2 (7 heaviest fawns)
October 28:	Spike buck introduced 10-30 min./day to each fawn	
November 1:	Ration for group 1 reduced to 70% (based on intake immediately prior to Nov. 1)	Ration for group 2 maintained *ad libitum*
December 18:	Groups joined, all animals on same feeding regime: 20% protein pellets + alfalfa. Released into one hectare research enclosure.	

cases the 48 day period of the experiment included parts of the self-accelerating phase as well as parts of the self-inhibiting phase of growth (each with a different instantaneous relative growth rate*). The reason for this was that the beginning of the feed restriction was not always exactly identical with the inflection point**, which was unknown when the experiment was started.

On December 18th, 1973 the experiment was terminated and the animals were released into the large research enclosure. By doing this, several parameters were altered:

1. Instead of being kept in small individual pens the animals were now able to utilize approximately 1 hectare.
2. Instead of being kept in isolation from each other, they were now able to interact socially, establish a ranking order, etc.
3. Instead of 1 buck (1 1/2 years old) being introduced for only a very short period daily, they were now constantly in the company of this same buck, 8 fawn bucks (approx. 6 months old) and an adult buck (age undetermined).
4. All animals, including the low weight group, ate at the common feeding trough and hay rack after December 18th and were, therefore, on an _ad libitum_ diet of 20% protein pellets and alfalfa hay.

Due to vandalism, on January 27th, 1974 the deer escaped from the research enclosure and lived in the forest from a few days to up to 3 weeks. On February 18th, 1974 the last one was

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* $k = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$ (Brody, 1964)

** See "Results and Discussion", Section C. Growth recaptured and the 14 experimental deer were placed again into their individual pens which they had occupied until December 18th. They had no more access to males, their diet was an *ad libitum* diet of 20% protein Calf Starter Pellets and alfalfa hay. The 14 does were kept individually until and during the fawning season of 1974 and for some time thereafter. They were released together with their fawns into the research enclosure on September 11th, 1974. On October 1st, 1974 5 fawns (hand-raised in 1974) were also released into this enclosure. All deer lived there in a group throughout the mating season of 1974* and during the winter and early spring of 1975. The feed remained unchanged until the end of February 1975, when it was altered to 16% protein Full-Flow Dairy Pellets plus alfalfa hay. In early May 1975 all females (year classes 1973 and 1974 plus 1 adult) were brought into the individual pens and kept there during the fawning season of 1975. At the end of June they and their fawns were released into the research enclosure, with 4 exceptions: doe #0-B which was kept separate until September since it only gave birth on August 21st, 1975 and 3 does (#0, I, 10) which were kept with their fawns in individual stalls until January 1976 for lactation studies.

In May 1975 the diet for all animals was changed back to 20% protein Calf Starter Pellets plus alfalfa hay. This was continued until September 1975 when the herd was divided into 2 groups for experimental purposes. From then on (during protein reduction experiment) the feeding regime was as shown in Table XII.

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*The mating season of a given year may extend to the early part of the following year.

Table XII - Regime for protein reduction experiment 1975 - 1976

Prior to September 4:	All animals on 20% protein pellets (+ alfalfa)	
September 4:	Herd divided into two groups:	
	Group 1 (High Protein) (including female fawns 16-B, 16-C, 17-B, 17-C*, 18-A*, 22-C)	Group 2 (Low Protein (including female fawns 3-C, 5-C, 19-A, 23-C, 31-A, I-B)
	20% prot. pellets + alfalfa	15% prot. pellets
September 24:	20% prot. pellets + alfalfa	10% prot. pellets
November 21:	16% prot. pellets + alfalfa	7% prot. pellets
December 24:	16% prot. pellets + alfalfa	10% prot. pellets
March 22:	Groups joined, all animals on same feeding regime: 16% protein pellets + alfalfa	

*Killed by dogs during course of experiment

In this experiment the effect of the restriction of one nutrient only, namely protein, was investigated. The total caloric value of the ration was maintained the same throughout the experiment (approx. 3,167 kcal/kg digestible energy; Hicks, pers. comm., 1977). Of all the specific nutritive components (protein, carbohydrates, lipids, high quantity minerals, vitamins, trace elements) that can possibly influence the attainment of puberty, protein was chosen because there is plentiful evidence that protein is especially important to the growth, health and reproduction of deer (see "Materials and Methods", section D. Feeding after Weaning). In this study an experimental group of 6 female fawns* (3 mother-raised, 3 hand-raised) was maintained from September 4th, 1975 to March 22nd, 1976 on a protein reduced diet. It was attempted to approximate the reduction in protein occurring in natural deer browse species during fall and winter. On Vancouver Island the crude protein content drops from an average high of ca. 17%, i.e. 6 - 35%, in late spring to an average low of ca. 6%, i.e. 2 - 9%, in winter (Gates, 1968; Rochelle, pers. comm., 1976).

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*Of these, 1 fawn (#31-A) was not used in weight gain comparison because of insufficient data.

RESULTS AND DISCUSSION

A. Birth Weight and Sex Ratios of Captive Fawns

The birth data* of the individual fawns (sex, birth date, birth weight, heart girth and hind foot measurements at birth, plus the age and weight of the dam and whether she was primiparous or pluriparous) are given in Appendix E. Only birth weights will be used for further comparison here as the heart girth and the hind foot data were not sufficiently complete.

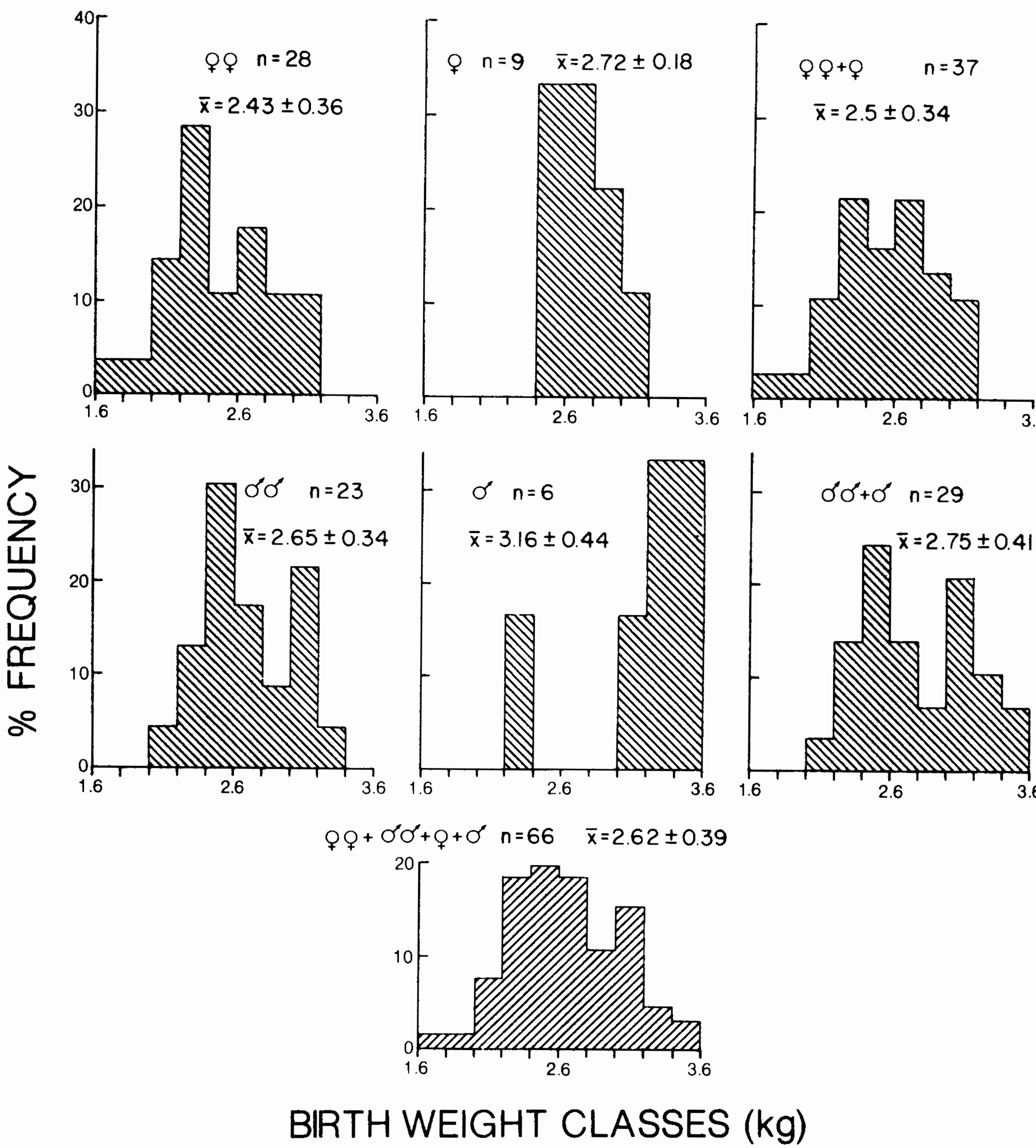
The frequency distributions of birth weights are shown in Figure 4. Single female fawns were found to be significantly heavier at birth than twin female fawns (t= 2.30, 35 d.f., $P < 0.05$) and single male fawns were significantly heavier than twin male fawns (t=3.0, 27 d.f., $P < 0.01$). Also, twin male fawns were significantly heavier than twin female fawns (t=2.21, 49 d.f., $P < 0.05$), and single male fawns were significantly heavier than single female fawns (t=2.75, 13 d.f., $P < 0.01$). Since the majority of single fawns (15 of 20, Kelsey Bay stock and Washington stock) was born to yearling dams which had not yet attained their full size and weight at this parturition, it follows that some of the heaviest fawns were born to the lightest dams. This phenomenon persisted at 2 and 3 years of age. Dams who had been precocious were consistently lighter than non-precocious dams and their subsequent fawns were heavier at birth

*The term "birth data" does not necessarily mean the data collected immediately after birth (which often happened at night) but within 24 hours of birth.

Figure 4 - Histograms of frequency distributions of fawn birth weights in captivity (1974 - 1976).

The weight class between 1.6 kg and 1.8 kg contains the weights from 1.6 kg to 1.79 kg, the weight 1.8 kg is included in the next weight class between 1.8 kg and 2.0 kg, etc.

The mean ± 1 S.D. is given for each group



The weight class between 1.6 and 1.8 contains the weights from 1.6 to 1.79 kg., the weight 1.8 kg. is included in the next weight class between points 1.8 and 2.0 etc.

than those of precocious dams (Table XIII). Statistical comparison was not done because of small sample sizes. Why the fawns of early breeders continued to be heavier than those born to late breeders is difficult to explain. It is most likely that this difference is an artifact due to the small sample sizes.

In all cases single fawns were born to primiparous dams; pluriparous dams always gave birth to twins. However, in 8 cases (of 13) primiparous 2 year olds also gave birth to twins; in 1 case (of 16) even a primiparous yearling gave birth to healthy twins. (These figures are not necessarily the same as in Table XIII, because additional animals were included whose weights and measurements at birth were unknown.)

It is interesting to note that in a sample of 33 pairs of twin black-tailed deer fawns collected at N. W. Bay from 1950 to 1962 (Bandy, pers. comm., 1975) the proportion of male to female to mixed sex twin sets was very similar to that found in the experimental herd from 1974 to 1976, as was the proportion of all males to all females (Table XIV).

B. Parturition Dates

The first births that occurred in the experimental herd in 1974 were to females of Kelsey Bay stock which were 1 year old (one exception: adult doe #0, of different origin). It was found that the parturition dates in 1974 were spread over a period of almost 2 months and were, in general, later than the normal fawning time of the species in the vicinity of Kelsey Bay

Table XIII - Birth weights of fawns in relation to dams' weights at parturition (in kg)

Males		Females	
Single fawns born to yearlings	Single fawns born to 2 yr. olds (who did not give birth as yearlings)	Single fawns born to yearlings	Single fawns born to 2 yr. olds (who did not give birth as yearlings)
Dam: 38.06 ± 5.97(5) Fawn: 3.33 ± 0.13(5) D/F = 11.43	Dam: 45.5(1) Fawn: 2.3(1) D/F = 19.78	Dam: 36.57 ± 2.6(6) Fawn: 2.79 ± 0.18(6) D/F = 13.10	Dam: 44.46 ± 3.2(3) Fawn: 2.58 ± 0.06(3) D/F = 17.23
Twin fawns born to 2 yr. olds (who gave birth as yearlings)	Twin fawns born to 2 yr. olds (who did not give birth as yearlings)	Twin fawns born to 2 yr. olds (who gave birth as yearlings)	Twin fawns born to 2 yr. olds (who did not give birth as yearlings)
Dam: 41.1 ± 3.6(8) Fawn: 2.71 ± 0.29(10) D/F = 15.17	Dam: 42.05 ± 1.6(2) Fawn: 2.5 ± 0.1(3) D/F = 16.82	Dam: 40.59 ± 2.9(9) Fawn: 2.3 ± 0.37(12) D/F = 17.65	Dam: 44.8 ± 4.1(3) Fawn: 2.22 ± 0.27(5) D/F = 20.18
Twin fawns born to 3 yr. olds (who gave birth as yearlings)	Twin fawns born to 3 yr. olds (who did not give birth as yearlings)	Twin fawns born to 3 yr. olds (who gave birth as yearlings)	Twin fawns born to 3 yr. olds (who did not give birth as yearlings)
Dam: 47.6 ± 5.7(4) Fawn: 2.85 ± 0.52(5) D/F = 16.70	Dam: 54.5(1) Fawn: 2.35 + 0.21(2) D/F = 23.19	Dam: 45.72 ± 3.2(6) Fawn: 2.66 ± 0.33(9) D/F = 17.19	Dam: 45.5(1) Fawn: 2.45 + 0.7(2) D/F = 18.57

In most yearling dams weight in September (Appendix E)
D/F = Dam/Fawn ratio

Table XIV - Fawn sex ratio

Experimental deer								Wild deer			
Twin births				Single births				Twins captured at North West Bay 1959 - 1962 (Bandy, pers. comm.)			
# of fawns ♂	# of fawns ♀	# of births	% of total	# of fawns ♂	# of fawns ♀	# of births	% of total	# of fawns ♂	# of fawns ♀	# of births	% of total
16	16	16	42	9		9	45	15	15	15	46
22	-	11	29		11	11	55	20		10	30
-	22	11	29						16	8	24
38	38	38	100	9	11	20	100	35	31	33	100

(N. W. Bay: Thomas, 1970) and at Kelsey Bay itself (Figure 5) and later than the fawning time in the experimental herd in 2 subsequent years (Figure 5). Young (yearling) black-tailed deer in the wild breed* later than the adults and their dates of ovulation are more variable (Thomas, 1970). Swank (1958) found yearling Arizona mule deer to breed 1 month later than adults. In this study little difference was found between the mean date of parturition of captive yearlings and adults for the years 1975 and 1976 when this comparison could be made. This follows Thomas' (1970) findings at N. W. Bay, where the mean date of second ovulation (= mean date of conception) in yearlings was only one day later than in adults (Figure 4). The variability of parturition dates was somewhat greater in yearlings (n=5, S.D.=7.81) than in adults (n=13, S.D.=5.01) in 1976, the only year when a meaningful comparison could be made, but this difference was not statistically significant.

In 1975 the mean date of parturition in the captive herd was earlier than that of the wild population in the vicinity of Kelsey Bay (June 14th: Thomas, 1970**) and at Kelsey Bay (June 9th: this study) and earlier than that of the captive herd in 1974 (unusually late) and 1976, when it was similar to that of

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*Taber, 1953: estimation of mating dates from ages of fetuses in dead does; Hines, 1968: calculation of mating dates from observed parturition dates; Thomas, 1970: estimation of dates of second ovulation, at which 96% of does conceived, from changes in ovarian structures

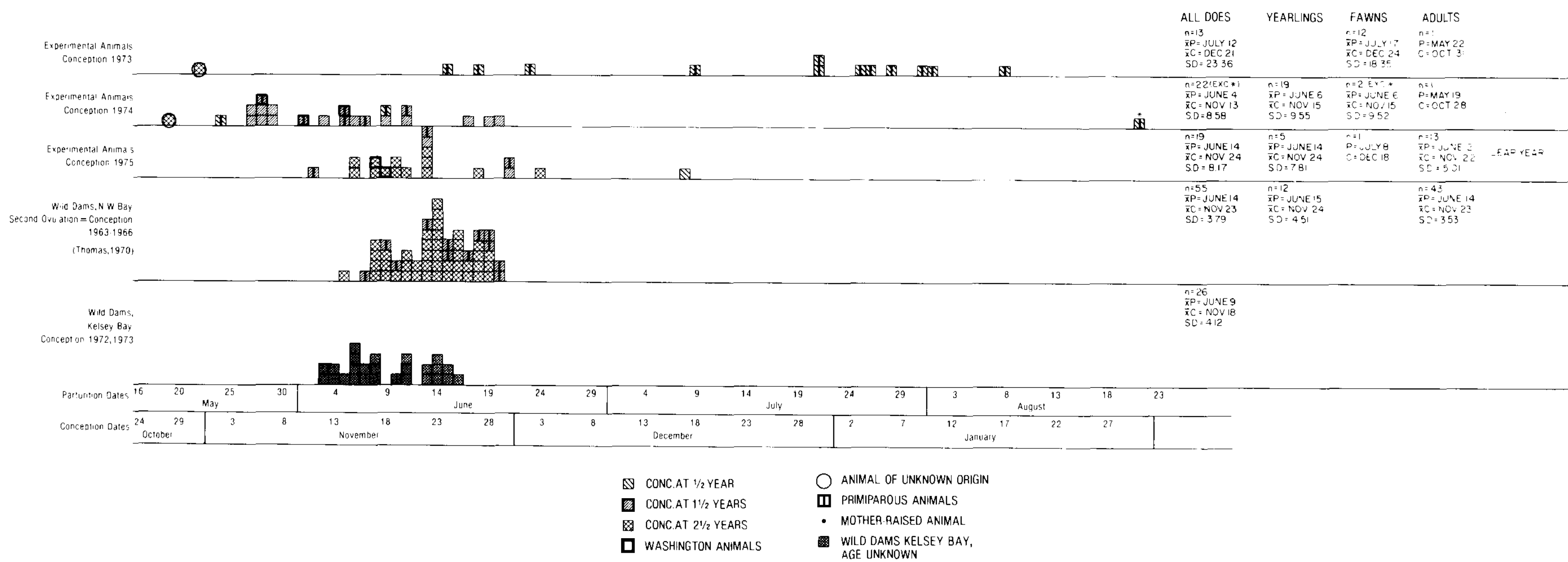
**Thomas stated that during the period from 1959 to 1964, from which this mean is derived, only insignificant differences occurred between the distributions for each year.

Figure 5 - Distribution of parturition and conception dates of experimental and wild black-tailed deer.

Conception dates: one day before actual or calculated (in wild dams) parturition minus 203.

Parturition dates for Thomas' data: estimated dates of second ovulation plus 204.

$\bar{x}P$: mean parturition date
$\bar{x}C$: mean conception date



Experimental Animals Conception 1973
Experimental Animals Conception 1974
Experimental Animals Conception 1975
Wild Dams, N W Bay Second Ovulation = Conception 1963-1966
(Thomas, 1970)
Wild Dams, Kelsey Bay Conception 1972, 1973
ALL DOES
YEARLINGS
FAWNS
ADULTS
n=13 x̄P = JULY 12 x̄C = DEC 21 SD = 23.36
n=12 x̄P = JULY 17 x̄C = DEC 24 SD = 18.35
n=1 P = MAY 22 C = OCT 31
n=22 (EXC *) x̄P = JUNE 4 x̄C = NOV 13 SD = 8.58
n=19 x̄P = JUNE 6 x̄C = NOV 15 SD = 9.55
n=2 EXC * x̄P = JUNE 6 x̄C = NOV 15 SD = 9.52
n=1 P = MAY 19 C = OCT 28
n=19 x̄P = JUNE 14 x̄C = NOV 24 SD = 8.17
n=5 x̄P = JUNE 14 x̄C = NOV 24 SD = 7.81
n=1 P = JULY 8 C = DEC 18
n=13 x̄P = JUNE 3 x̄C = NOV 22 SD = 5.01
LEAP YEAR
n=55 x̄P = JUNE 14 x̄C = NOV 23 SD = 3.79
n=12 x̄P = JUNE 15 x̄C = NOV 24 SD = 4.51
n=43 x̄P = JUNE 14 x̄C = NOV 23 SD = 3.53
n=26 x̄P = JUNE 9 x̄C = NOV 18 SD = 4.12
Parturition Dates
16 20 25 30 May
4 9 14 19 24 29 June
4 9 14 19 24 29 July
3 8 13 18 23 August
Conception Dates
24 29 October
3 8 13 18 23 28 November
3 8 13 18 23 28 December
2 7 12 17 22 27 January
CONC. AT 1/2 YEAR
CONC. AT 1 1/2 YEARS
CONC. AT 2 1/2 YEARS
WASHINGTON ANIMALS
ANIMAL OF UNKNOWN ORIGIN
PRIMIPAROUS ANIMALS
MOTHER-RAISED ANIMAL
WILD DAMS KELSEY BAY, AGE UNKNOWN

the wild population (Figure 5).

C. Growth

1. Growth in relation to puberty.

It is well-known that in mammalian females, puberty is more closely related to weight than to age. In rats (Ershoff, 1952; Widdowson and McCance, 1960; Widdowson *et al.*, 1964; McCance, 1962; Kennedy, 1969; Kennedy and Mitra, 1963), mice (Barnett and Coleman, 1959; Monteiro and Falconer, 1966), rabbits (Myers and Poole, 1962), pigs (Dickerson *et al.*, 1964), cattle (Crichton *et al.*, 1959; Joubert, 1963), sheep (Hafez, 1952; Allen and Lamming, 1961), white-tailed deer (Lenker and Scanlon, 1975) and humans (Frisch, 1974), it has been found that puberty, defined by vaginal opening (in rodents), by first estrus (in ungulates) or by menarche (in humans) is attained at the same mean weight by slowly growing individuals, as by rapidly growing ones, but at a significantly higher age by those that grow slowly.

In a study investigating the precocious attainment of puberty it was, therefore, necessary to monitor that part of the development of the somatic tissue which is manifested as growth, i.e. as an increase in body size.

In Table XV regression formulae describing growth curves are compared for females who subsequently produced fawns as yearlings and those who did not. The reasons for utilizing these particular formulae are described later in this section. In deriving these formulae data points on the self-accelerating phase

Table XV - Comparison of individual growth formulae of precocious and non-precocious breeders

			$\ln Y = A + B_1 t + B_2 \left(\frac{1}{t+10}\right)$			Y = A + Bt		Y = A + Bt	
			Y = Body Wt (kg)			Y = Hind Foot Length (cm)		Y = Heart Girth (cm)	
Tag #	Max. age for which data were used (in days)	Determined by	A	B_1	B_2	A	B	A	B
			Precocious Breeders (n = 16)						
1	140	inflection point	1.671	0.012	-9.716	22.83	0.090	25.93	0.283
2	167	inflection point	2.320	0.008	-23.285	24.98	0.096	28.52	0.290
3	117	data limit	1.670	0.013	-9.734	23.5	0.108	28.00	0.272
8	110	data limit	1.468	0.014	-6.564	23.560	0.105	28.29	0.262
11	165	inflection point	2.179	0.009	-21.299	24.83	0.091	30.32	0.268
14	137	inflection point	1.743	0.012	-12.124	23.386	0.097	26.36	0.275
15	163	inflection point	2.303	0.008	-23.601	24.654	0.093	29.07	0.267
16	146	inflection point	1.563	0.012	-8.664	22.68	0.088	27.157	0.275
17	146	inflection point	1.517	0.014	-8.796	22.186	0.105	26.027	0.304
21	149	inflection point	1.481	0.013	-8.018	22.646	0.106	25.795	0.283
22	115	data limit	1.534	0.015	-6.646	22.34	0.108	28.95	0.274
23	144	inflection point	1.485	0.014	-7.079	22.317	0.105	22.733	0.346
E	167	inflection point	2.017	0.008	-14.218	21.217	0.119	25.62	0.310
I	176	inflection point	2.464	0.007	-25.922	24.18	0.110	28.02	0.304
16-C	113	data limit	1.256	0.017	-3.192	23.287	0.121	28.184	0.328
<u>0-B</u>	164	data limit	1.337	0.019	-2.649	no data		no data	
		max.	2.464	0.019	-25.922	24.980	0.121	30.320	0.346
		min.	1.256	0.007	-2.649	21.217	0.088	22.733	0.267
		$\bar{x}$	1.751	0.012	-11.969	22.412	0.103	27.265	0.290
			Non-Precocious Breeders (n = 12)						
10	161	inflection point	1.925	0.011	-13.827	24.66	0.096	29.20	0.286
18	178	inflection point	1.622	0.014	-9.638	24.01	0.102	26.497	0.305
19	129	inflection point	1.857	0.010	-15.504	23.11	0.091	27.37	0.256
24	117	inflection point	1.614	0.014	-7.344	22.839	0.110	26.93	0.300
F	167	inflection point	2.573	0.005	-25.763	23.60	0.105	29.98	0.240
J	167	inflection point	2.089	0.009	-15.301	23.303	0.119	27.169	0.310
I-B	114	data limit	1.475	0.013	-8.603	22.185	0.108	28.485	0.254
3-C	97	data limit	1.639	0.014	-8.122	23.322	0.126	29.735	0.339
<u>5-C</u>	93	data limit	1.889	0.010	-8.689	insuff. data		insuff. data	
<u>17-B</u>	105	data limit	1.270	0.027	-8.296	20.07	0.147	25.189	0.335
<u>16-B</u>	85	data limit	1.713	0.015	-8.447	insuff. data		insuff. data	
<u>23-C</u>	107	data limit	1.300	0.016	-7.006	20.672	0.127	25.855	0.307
		max.	2.573	0.017	-25.763	24.660	0.147	29.980	0.339
		min.	1.270	0.005	-7.006	20.070	0.091	25.189	0.240
		$\bar{x}$	1.747	0.012	-11.428	22.777	0.113	27.641	0.293

Correlation coefficient r was always significantly ($P<0.001$) different from zero correlation and was approaching 1 in all cases.

Tag # of mother-raised fawns underlined.

of growth were used, as it is likely that if differences in somatic growth were to be found, they would appear more clearly during the phase of rapid weight gain. The upper age limit of data used in these curves was either a) the determined point of inflection of the weight growth curves or, in some cases, b) the age at which regular collection of weight data had ceased which, in every case, was prior to inflection. The inflection points were established by methods similar to those used by Bandy (1955). The mathematical method in this study used the calculations of absolute weight gain over constant periods of 7 days. The inflection point was considered to be the mid-point of the first 7 day period at which the weight gain fell below 1.0 kg and thereafter consistently remained below this level. This is slightly different from Bandy's (1955) mathematical determination of the inflection point, which he considered to be "marked by a change from increasing gains to decreasing gains" (p. 22). The graphical method approximated the inflection point by inspecting the weight growth curve on arithlog coordinate paper. Again, this method differed slightly from that used by Bandy in that it did not select the inflection point as "the point of consistent deviations of the actual observations from the straight line" (Bandy, 1955, p. 24) but as the point where the steep slope of the curve changed to a consistently flat slope. The inflection points found by the graphical method in this study were identical with those found by the mathematical method.

The graphs of the growth curves were produced by plotting weight against age on arithlog coordinate paper which resulted, in many cases, in straight lines for the self accelerating phase of growth. However, in some cases of weight growth the result was a curved line (Figure 6).

Brody (1964) has given an extensive and detailed review of methods of describing mammalian growth curves during the self-accelerating phase of growth. The most common form of equation used is $Y = Ae^{Bt}$ (Y = body measurement at time t, A = body measurement when t = 0, i.e. intercept; B = instantaneous relative growth rate, i.e. slope). This can be rewritten for easier computation as $\ln Y = \ln A + Bt$ in the form of the usual linear regression. This formula was used by Bandy (1965) to describe the self-accelerating portion of weight growth curves of black-tailed deer.

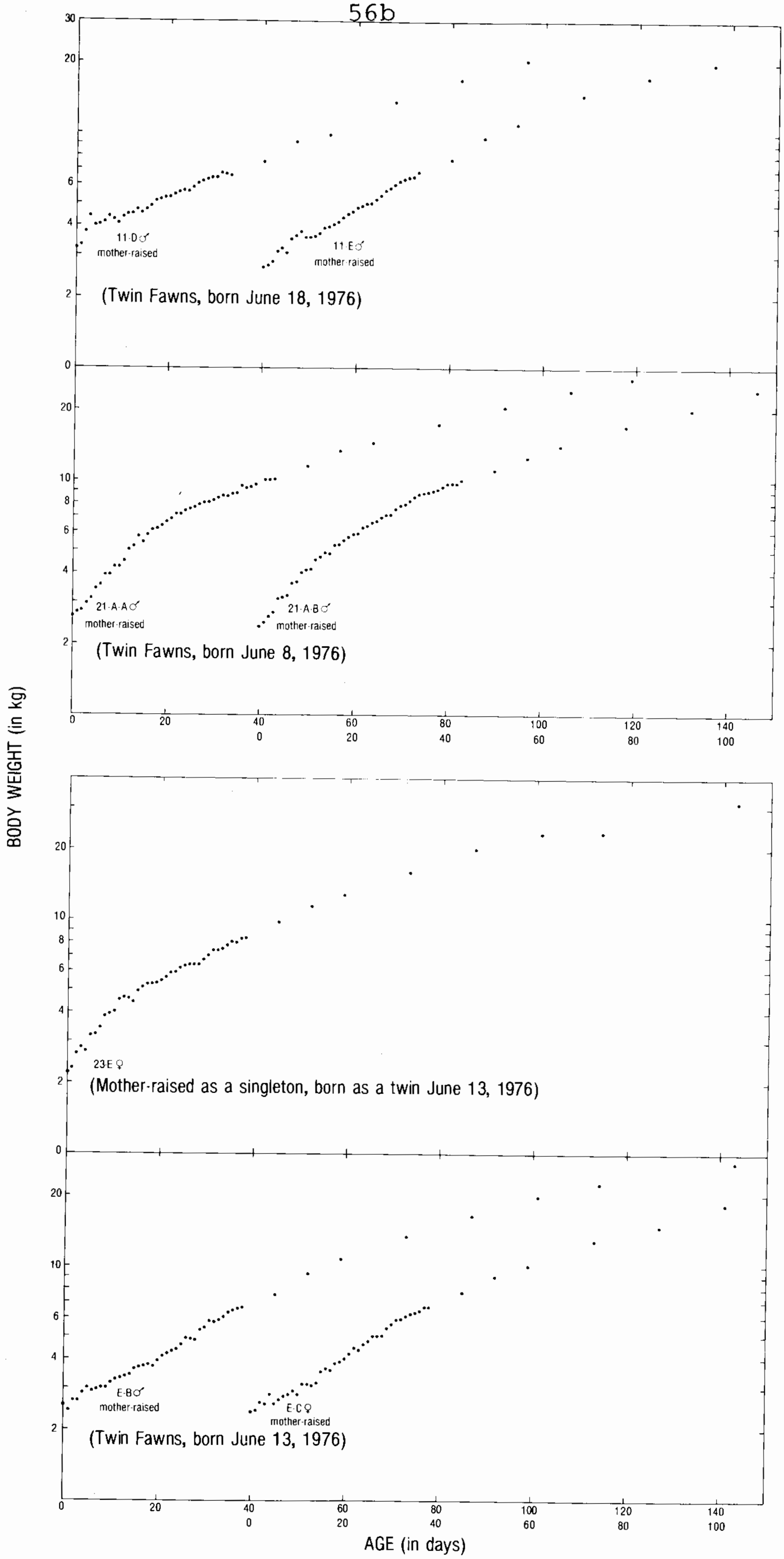
The plotting of data in this study showed that this type of curve did not describe weight growth very accurately for all animals. A recent paper by Anderson _et al_. (1974) noted that "there is no universally acceptable theoretical model for predicting growth over time" (p. 14), so instead, these workers attempted empirically to fit growth curves of mule deer (_O. h. hemionus_) to several different equations and to several types of transformations of body measurement and age. After detailed consideration of this approach, the weight data from each individual experimental deer obtained in this study were separately fitted, by the method of least squares (Snedecor and Cochran, 1967) to the following formulae: 1. $\ln Y = A+Bt$; 2. $\ln Y = A+B\left(\frac{1}{t+10}\right)$; 3. $\ln Y = A+B_1 t+B_2\left(\frac{1}{t+10}\right)$. The $\frac{1}{t+10}$ transformation was found

Figure 6 - Examples of variation in weight growth curves.

All fawns used were mother-raised, born June 1976, born as twins (sibling of 23-E removed at birth).

11-D/11-E cf. 21-A-A/21-A-B compares phased growth with steady growth.

23-E cf. E-B/E-C compares fast growth with slow growth.


BODY WEIGHT (in kg)
11-D♂ mother-raised
11-E♂ mother-raised
(Twin Fawns, born June 18, 1976)
21-A-A♂ mother-raised
21-A-B♂ mother-raised
(Twin Fawns, born June 8, 1976)
23E ♀
(Mother-raised as a singleton, born as a twin June 13, 1976)
E-B♂ mother-raised
E-C♀ mother-raised
(Twin Fawns, born June 13, 1976)
AGE (in days)

uniformly good by Anderson et al. (1974). In this study the 3rd formula was found to give the best fit to the weight data for every individual experimental deer. The highest r^2 values were obtained and the largest F ratio resulted from the analysis of variance (testing H_O: B = 0 against H_A: B ≠ 0; Zar, 1974). In all cases r^2 and F were highly significant (P < 0.001).

The heart girth and hind foot data were also fitted repeatedly for each individual experimental deer to the formulae:

1. $Y = A+Bt$; 2. $Y = A+B\ (\frac{1}{t+10})$; 3. $Y = A+B_1t+B_2\ (\frac{1}{t+10})$.

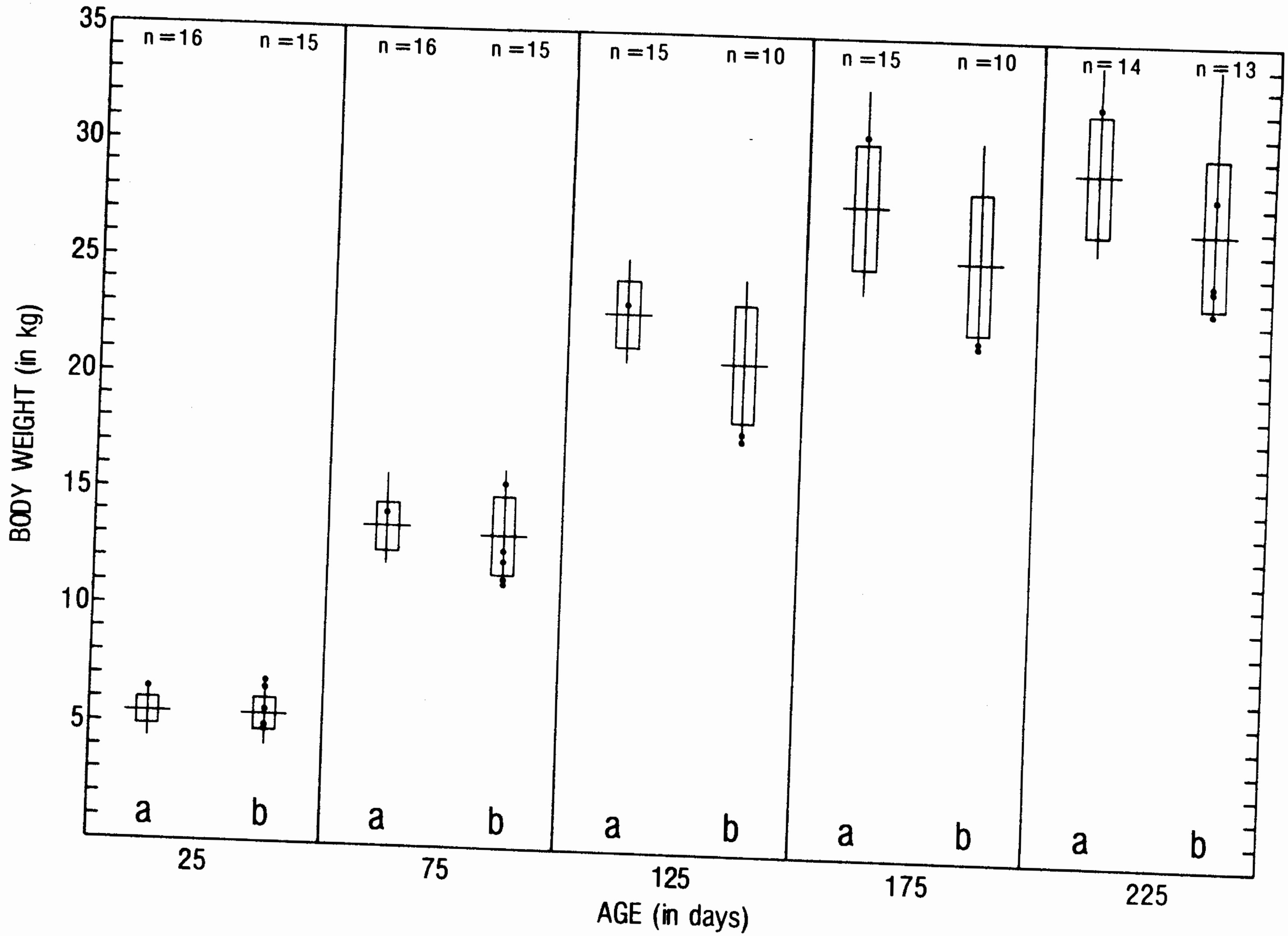
For every individual the first formula was found to give the best fit to both the heart girth and the hind foot data by similar criteria of r^2 and F. In all cases r^2 and F were highly significant (P < 0.001). The values for the best descriptive formulae are given for each deer in Table XV. This Table shows that the average growth curves were almost identical for precocious and non-precocious deer and, more importantly, that the maximum and minimum values were similar. This means that the early growth patterns of precocious breeders do not differ from those of non-precocious breeders.

A second comparison between the growth of females which were subsequently found to have bred as fawns and those who had not was done by comparing the weights achieved at 50 day intervals between the age of 25 to 225 days (Figure 7) and by comparing the times required to double the birth weight. This comparison of the weights at certain ages not only includes weights within the self-accelerating phase of growth but also weights beyond the inflection point (at 117 - 178 days) and within a major por-

Figure 7 - Comparison of body weights of precocious and non-precocious fawns at different ages.

Vertical bar represents range of observations. Block represents 1 S.D. on either side of the mean, which is shown as small horizontal bar.

Weights of mother raised fawns (dots) included in total sample.



a: Precocious Fawns b: Non-Precocious Fawns Dots indicate mother-raised Fawns tion of that phase of growth which Brody (1964) designated as the self-inhibiting phase. It also includes the point within this phase at which conception took place in the precocious animals (one exception: #0-B). Although the mean weights achieved at 25 days were identical for both groups (5.4 kg), as the fawns increased in age the precocious breeders became heavier. These weight differences were significant at 125 ($t=2.57$, 23 d.f., $P < 0.01$), at 175 ($t=1.92$, 23 d.f., $P < 0.05$) and at 225 days ($t=2.14$, 25 d.f., $P < 0.05$) of age. The change in weights and the differences between them were similar to the weight growth curves for early and late maturing children presented by Brody (1964) which also showed lower average weights for the late maturing individuals. However, although the average weights for early and late breeding fawns were found to be significantly different from 125 days of age onward, it is clear from inspection of Figure 7 that many non-precocious fawns achieved weights which exceeded not only the minimum but also the average prepubertal and pubertal weights of precocious fawns.

The average time required to double the birth weight, a measure of immediate post-natal growth, was not significantly different in the two groups. In this study the range was from 13 to 28 days for precocious, and non-precocious fawns combined. The mean was 19 days for the former and 18 days for the latter. The similarity in the times required to double the birth weight is in accordance with the identical average weight achieved at 25 days by both groups. Cowan and Wood (1955) found the time required by the black-tailed deer fawn to double its weight to range from 10 to 14 days.

A third comparison between precocious and non-precocious does was made by comparing the weights achieved at the end of the first breeding season of their lives expressed as percentage of the adult weights. The former value was considered to be the weight of each fawn on January 17th which had been calculated as the date when the last known precocious conception (one exception: #0-B, January 30th) took place, and the latter value as the weight immediately after parturition at 2 years of age. It is known (Anderson et al., 1974) that does continue to grow slowly until about 8 years of age, so that the weight at 2 years is not the true asymptotic weight. However, as growth is slow after the 1st year, the 2 year weight is a good approximation of mature weight and the best that could be obtained in this study.

Three does from Washington State, who were considerably larger at the same age than the Kelsey Bay stock animals (Bandy, 1955), were included in this comparison because only percentages were to be compared. Although the average of the precocious breeders was significantly higher ($t = 3.727$ d.f. $= 20$, $P < 0.01$)* than that of the non-precocious breeders (Table XVI), the values of many of the latter exceeded the minimum values of the former. This result is in accordance with the result of the comparison of absolute values at certain ages (Figure 7) and both results exclude the possibility of a simple threshold effect of weight (absolute or as proportion of adult weight) on the attainment of puberty. However, it should be pointed out that

*An arcsine transformation was used (Zar, 1974).

Table XVI - Comparison of weight at end of first breeding season[1] in relation to achieved adult weight[2] of precocious and non-precocious breeders

Precocious

	Tag #	Wt. first breed. season (kg)	Adult Wt. (kg)	%
1973	2	32.3	44.9	71.9
	3	27.3	39.0	70.0
	5	29.9	40.4	74.0
	8	29.1	40.5	71.9
	11	32.2	48.1	71.1
	14	29.8	38.2	78.0
	15	30.5	45.0	67.8
	16	25.8	38.8	66.5
	17	28.3	45.4	62.3
	22	28.6	41.7	68.6
	23	28.0	40.8	68.6
1974	E	26.2	37.7	69.5
			$\bar{x}$ =	70.0±3.9
			$\sin^{-1}x$ =	56.84±2.47

Non-precocious

	Tag #	Wt. first breed. season (kg)	Adult Wt. (kg)	%
1973	10	31.7	44.5	71.2
	18	34.0	48.1	70.7
	19	24.5	42.4	57.8
	24	25.9	40.8	63.5
1974	F	27.3	44.5	61.3
	J	27.2	42.7	63.7
	K	28.5	49.1	58.0
1973[3]	29	32.4	53.5	60.6
	30	36.2	55.8	64.9
	31	39.9	63.5	62.8
			$\bar{x}$ =	63.5±4.6
			$\sin^{-1}x$ =	52.84±2.76

(1): Wt. at January 17 = last date of conception for precocious fawns

(2): Immediate post-partum weight at 2 years of age

(3): Fawns from Washington State

the higher weights of the precocious fawns at the end of the first breeding season in relation to the adult weights were likely due in part to the negative effect of pregnancy on adult weights (Table XIII).

2. Growth in relation to nutrition

a) Variation in relation to milk nutrition

In an earlier study of growth in this species Cowan and Wood (1955) described 3 well-defined and separable phases of pre-pubertal growth. They noted that each of these phases were characterized by a constant instantaneous relative growth rate ($k = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$, Brody, 1964) the value of which decreased in subsequent phases. Detailed examination of the growth curves collected in this study did not reveal such a consistent pattern of growth for all individuals. While some animals showed growth patterns which resembled those described by Cowan and Wood (1955), others differed in having more or less than 3 phases as demonstrated on some typical examples in Figure 6. In the same paper Cowan and Wood (*ibidem*) also stated that the nutritive quality of the doe's milk during the first phase of growth, when the instantaneous relative growth rate is highest (Figures 6, 8 and 9) "must be superlative" (p. 334). Milk was sampled from 2 primiparous does (#10: 2 yrs. old, #I: 1 yr. old) throughout lactation (Appendix C) each nursing a male fawn which showed a high rate of growth after birth (#I-A: K = 0.057, 0 - 8 days; #10-A: K = 0.057, 0 - 7 days). This, however, was not as high as the rate found by Cowan and Wood (1955) or the maximum rate observed

Figure 8 - Fawn weight gain in relation to caloric value of milk.

Twin fawns, born June 9th, 1975 to primiparous, yearling doe.

Caloric value of doe's milk as weekly and bi-weekly averages.

Evaporated cow's milk: 1440 kcal/kg.

Doe's milk: caloric value calculated E=9F+4P+4L.

F(fat), P(protein), L(lactose): g/kg.

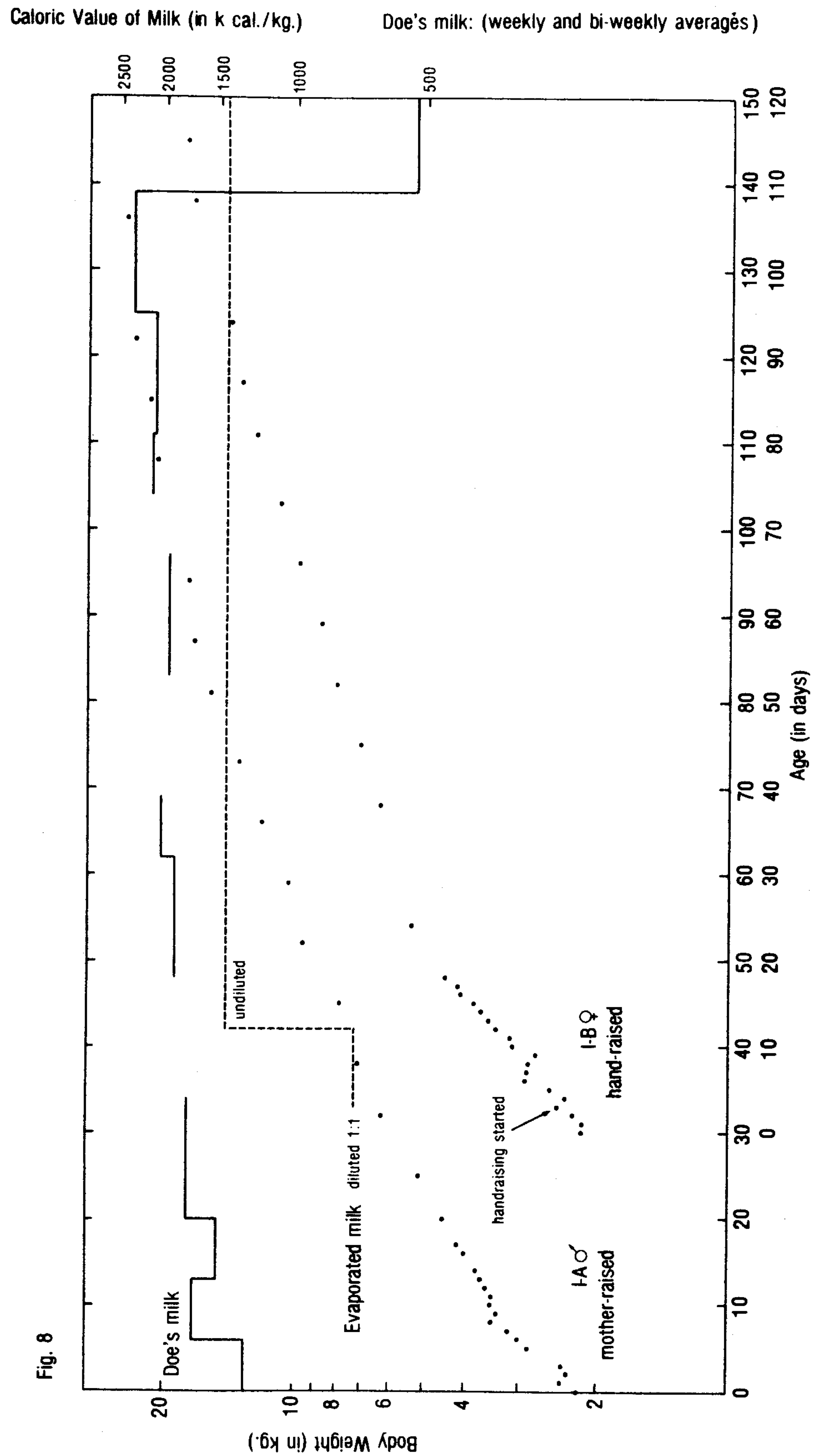

Caloric Value of Milk (in k cal./kg.)
Doe's milk: (weekly and bi-weekly averagês)
2500
2000
1500
1000
500
Doe's milk
Evaporated milk diluted 1:1
undiluted
handraising started
I-A ♂ mother-raised
I-B ♀ hand-raised
Body Weight (in kg.)
20
10
8
6
4
2
Age (in days)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
0
10
20
30
40
50
60
70
80
90
100
110
120

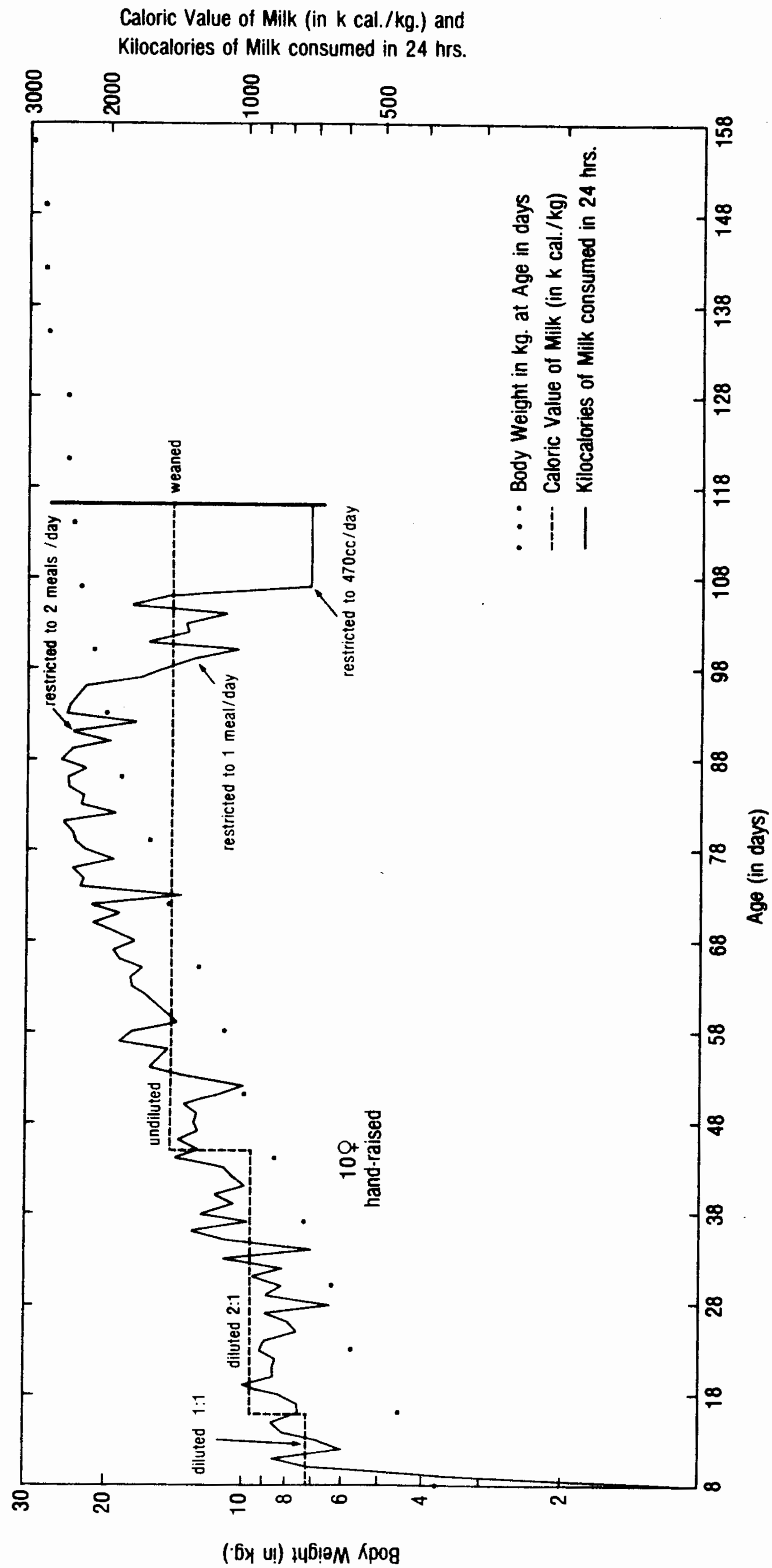
Fig. 8

Figure 9 - Fawn weight gain in relation to daily consumption of milk calories and caloric value of milk.

Evaporated cow's milk: 1.44 kcal/g

1 ml = 1.068g = 1.538 kcal

Fig. 9


Caloric Value of Milk (in k cal./kg.) and
Kilocalories of Milk consumed in 24 hrs.
3000
2000
1000
500
Body Weight (in kg.)
30
20
10
8
6
4
2
Age (in days)
8
18
28
38
48
58
68
78
88
98
108
118
128
138
148
158
• • • Body Weight in kg. at Age in days
---- Caloric Value of Milk (in k cal./kg)
— Kilocalories of Milk consumed in 24 hrs.
10♀
hand-raised
diluted 1:1
diluted 2:1
undiluted
weaned
restricted to 2 meals /day
restricted to 1 meal/day
restricted to 470cc/day

in this study, namely $K \approx 0.1$ per day.

In both cases the caloric value of the milk was actually lower in the first week of lactation (doe #10: 1466 kcal/kg; doe #I: 1280 kcal/kg) than it was in later lactation (doe #10 ranged from 1685 kcal/kg at week 2 to 1947 kcal/kg at weeks 14 and 15, doe #1 from 1692 kcal/kg at week 2 to 2364 kcal/kg at weeks 19 and 20). It would thus appear that the rapid early growth of fawns is not due to a "superlative" quality of the does' milk. In addition it was found that there was no direct correlation between the relative caloric content of milk formulae used in hand-raising fawns and their growth rates. The youngest fawns were fed evaporated milk diluted 1:2 with water, and as they grew the dilution was reduced resulting in an increased caloric value of the formula fed. However, growth rates were highest on the most diluted milk (Figures 8 and 9).

It appears that the extraordinary weight gains during the initial growth phase occurring in fawns must be attributed not to the higher quality of the does' milk during that phase but to the fawns' ingestion of proportionality greater quantities of milk, resulting in a higher total intake of calories. Ongoing studies on the energy transfer from the dam to the fawn which include quantitative measurements of the milk should shed more light on this problem.

b) Experimental alteration of nutrition

i. Reduction of total intake

No attempt was made in this study to reduce fawn growth by lowering the plane of nutrition during the nursing period. It is possible to retard the growth of animals by limiting the intake of nutrients during their rapid phase of growth and thus delay puberty in these stunted animals, as puberty is weight-dependent (references see section "Growth in relation to puberty"). However, such an experiment would hardly be relevant to this study. It is not probable that of the large number of female black-tailed deer found not to breed as fawns (Thomas, 1970; Jordan and Vohs, 1976) all had been retarded by inadequate nutrition during their early growth. Instead, in 1973 the quantitative intake of feed was restricted to 70% for a group of 7 hand-raised fawns at about the time when their weight growth curves had reached the inflection point, i.e. after their phase of rapid growth had been completed (Table XVII). This was done in order to simulate conditions in the wild, namely the decrease in deciduous browse as experienced by wild black-tailed deer in fall and winter.

It was found that the 70% plane of nutrition maintained during a 48 day period of late growth had no significant effect on the weight increase (in % of weight at inflection point). It also had no negative effect on the occurrence of precocious puberty which, in the 70% group was 5 in 6 and in the _ad libitum_ group 4 in 7 (experimental and control animals hand-raised). The probability exists that the _ad libitum_ group voluntarily restricted the food intake to approximately the same level as that available to the experimental group. Although it seemed that higher absolute weight had no positive influence on the attainment of puberty (70% group significantly lower mean weight: $t = 2.66$, 11 d.f., $P < 0.05$) this must be seen in the light of the overall result of

Table XVII - Influence of quantitatively restricted diet on late growth (Nov. 1-Dec. 18, 1973

Experimental group on 70% of mean daily intake one week before start of experiment

Control group on ad libitum intake

Type of feed: 20% protein Calf Starter Pellet (Buckerfield), alfalfa hay

A. 70% Group

Tag #	Age at Infl. Point of Wt. Growth Curve	Age at Beginning of Restriction	Weight at Beginning of Restriction	Age at End of Restriction	Weight at End of Restriction	Weight Increase in %
1*	140	143	25.1	191	28.0	11.6
16*	146	139	23.7	187	25.3	6.8
17*	146	138	25.6	186	27.1	5.9
19	129	136	23.2	184	24.4	5.2
21*	149	141	23.9	189	26.9	12.6
23*	144	143	26.4	191	27.8	5.3
					x = 26.6	$\bar{x}$ = 7.9 ± 3.3
					SD = 2.43	$\sin^{-1}x$ = 16.06 ± 3.4

B. Ad lib. Group

Tag #	Age at Infl. Point of Wt. Growth Curve	Weight at Infl. Point	Age at Infl. P. + 48 days	Weight at Age Infl. P. + 48 days	Weight Increase in %
2*	167	31.2	215	32.5	4.2
10	161	29.6	209	31.4	6.1
11*	165	30.0	213	33.5	11.7
14*	137	25.4	185	28.8	13.4
15*	163	28.9	211	29.8	3.1
18	178	30.8	226	34.0	10.4
24	117	22.6	165	24.1	6.6
				$\bar{x}$ = 30.6	$\bar{x}$ = 7.9 ± 3.9
				SD = 3.42	$\sin^{-1}x$ = 15.92 ± 4.27

Age in days - Weight in kilograms - Asterisks indicate animals who became pregnant.

One of the animals selected for group A died of an injury during the course of the experiment and is not included in this Table.

this study on a much larger sample which showed that precocious animals are heavier (Figure 7).

ii. Variation in protein content

It is quite clear that the rather crude method of protein reduction used in the 1975 experiment could only approximate the influence of the decline of protein in natural forage on the nutrition of deer, because it is insufficiently known a) to what degree deer counteract this decline by selective feeding and physiological adaptations such as urea utilization and b) what the ratio of digestible protein to crude protein is (references see "General Discussion and Conclusions"). Furthermore, in the experiment protein was only reduced in the solid food ingested by the fawns (and their dams). The protein level of the dams' milk was unknown, although it is safe to assume that it was high (Appendix C). This, however, is in accordance with the feeding regime of wild deer who experience a reduction in the protein content of browse while they are still nursing. As mentioned earlier, a control group of 4 fawns was maintained on a high protein diet while an experimental group of 6 fawns was fed a diet the protein content of which was progressively lowered (Tables XII and XVIII).

In order to compare the weight changes between the control and the experimental group, the changes between the 2 following points in time were calculated:

1. One hundred days of age. As fawns were of different ages when the experiment was started on September 4th, this was selected as a standard age. The oldest fawn was 100 days old on September 6th, the youngest one on September 27th.

2. The date of weighing nearest the end of the experiment on March 22nd, 1976.

As the animals had not been weighed regularly at the end of the experimental period, the second point was somewhat different for each animal. The weight changes were therefore recorded over periods of different length. In addition, the weights of the animals at 100 days of age were different. To standardize comparison the weight gains were expressed as the average daily weight gain in percent of the weight at 100 days. The weight at 100 days of age was chosen over the weight at the start of the experiment because it was thought that this would minimize the inevitable inaccuracies of this comparison. At the start of the experiment (September 4th) the animals were at very different stages of their growth, the rate of which was rapidly changing. Probably less inaccuracy was caused by selecting the weight at 100 days as standard weight. Although the animals had been on a protein-reduced diet for varying lengths of time at 100 days of age, the protein reduction at this point was minimal (15% from 20%) and so were, very likely, any effects possibly produced by it.

There was no significant difference in weight gains between the 2 groups (Table XVIII). However, no reproduction (parturition) occurred in any of the 6 fawns on the protein-reduced diet while 1 fawn in the high protein group became pregnant and subsequently gave birth. This result must be seen in conjunction with the high percentage of pregnancies in fawns on high protein diets throughout the study, which can all be considered controls to the low protein group.

Table XVIII - Influence of protein-reduced diet on growth and attainment of puberty (Sept. 4, 1975 - March 22, 1976)

Group	Tag #	100 days of age: Weight (kg)	100 days of age: Date	Date nearest to end of experiment: Weight (kg)	Date nearest to end of experiment: Date	Date nearest to end of experiment: Age (days)	% Wt. Gain/ Day	Period monitored (in days)	Progesterone (ng/ml)
Red. Prot. Group (15%-10%-7%-10%)	3-C	19.8	28-9	26.8	29-3	283	0.19	183	5.8
	23-C	16.8	25-9	24.5	5-3	261	0.30	161	5.4
	I-B	16.7	17-9	29.1	19-3	267	0.45	167	12.6
	5-C	15.8	11-9	25.5	5-3	276	0.35	176	11.2
	19-A	15.9	20-9	25.9	5-3	266	0.38	166	8.6
			x̄ = 20-9 SD = 6.7			x̄ = 271 SD = 8.8	x̄ = 0.33 SD = 0.10	x̄ = 171 SD = 8.8	
High Prot. Group (20%-16%)	17-B	16.6	27-9	29.5	2-3	256	0.50	156	7.7
	[16-C]	17.5	19-9	30.0	2-3	265	0.40	165	16.1
	16-B	21.0	19-9	29.1	2-3	265	0.23	165	3.8
	22-C	15.2	6-9	24.1	2-3	277	0.33	177	4.3
			x̄ = 18-9 SD = 8.7			x̄ = 266 SD = 8.6	x̄ = 0.37 SD = 0.12	x̄ = 166 SD = 8.6	

Age in days - Weight in kilograms - Mother-raised fawns underlined

Tag # boxed in indicates pregnancy

Blood progesterone levels were measured* but could not be compared to those of Abler *et al*. (1976) in white-tailed deer, as the breeding season was passed (late February) and any possibly existing difference in ovarian activity between the 2 groups most likely would have disappeared. However, it was found that the only fawn which subsequently gave birth had the highest progesterone level (Table XVIII). Ongoing studies will show whether blood progesterone levels can be used as an indicator of pregnancy in black-tailed deer. In white-tailed deer it was found (Plotka *et al*., 1977) that progesterone levels are similar for the major portion of pregnancy and the luteal phase of the estrous cycle, but higher at late pregnancy than at early pregnancy and during the estrous cycle.

iii. Mother-raised compared to hand-raised fawns

The precocious fawn which showed the highest progesterone level (#16-C) was one of a pair of female twins with identical birth weights (2.5 kg); it had been hand-raised while its sibling (#16-B) had been mother-raised. The mother-raised fawn grew faster than the hand-raised one (6.5 compared to 5.7 kg at 25 days; 15.5 to 13.2 kg at 75 days; 28.4 to 27.3 kg at 225 days). The higher weight of the hand-raised fawn at 265 days (30.0 compared to 29.1 kg) was probably caused by increased uterine weight due to pregnancy. A second pair of twins raised in the same manner and compared showed the opposite: the hand-raised fawn

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*Radioimmunoassay [Progesterone (^{3}H) Radioimmunoassay Pak, New England Biomedical Assay Laboratories] done by B. A. McKeown, S.F.U.

(#17-B) grew faster than the mother-raised fawn (#17-C). In this case neither of these fawns became pregnant although they were, as was the previous pair, both kept on a high protein diet. These 2 examples indicate that the rearing regime had no consistent influence on growth. This was generally confirmed when the weight-growth of all healthy mother-raised and hand-raised female fawns of Kelsey Bay stock was compared (Figure 10). Also included in this comparison were a doe not of Kelsey Bay stock (#0-B) but of similar, Vancouver Island parentage, and her 1976 offspring (#0-B-C). In addition, 7 of the fawns born in 1976 were included, although at the time of writing pregnancy had only been determined by x-ray and not by the actual occurrence of parturition. These animals had, therefore, not been included in comparisons of precocious and non-precocious breeders.

The comparison of weight growth in hand- and mother-raised animals showed that, although initially the mother-raised fawns grew faster (doubling of birth weight: $\bar{x}$ = 16 days/ $\bar{x}$ = 19 days, $t = 2.56$, 37 d.f., $P < 0.01$; weight at 25 days: $\bar{x}$ = 6.3kg/ $\bar{x}$ = 5.3kg, $t = 3.8$, 37 d.f., $P < 0.01$), no significant differences occurred at 75, 125 and 175 days of age. The initial growth difference was certainly caused by the fact that fawns lost some weight for a short time after being removed from their dams.

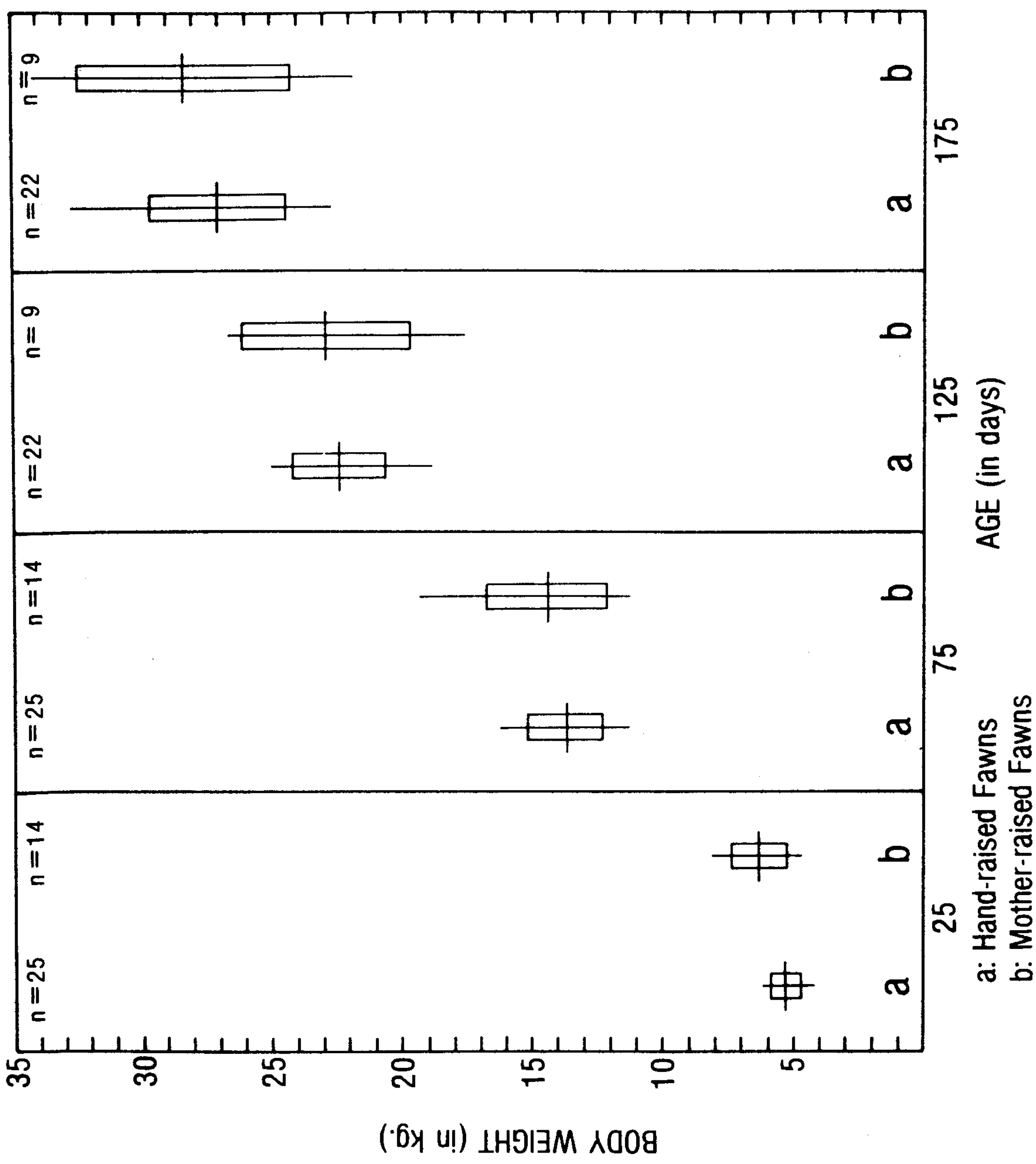
D. Puberty

In this study parturition was the only criterion used to determine whether puberty had been reached (except in 1976, when pregnancy was used). Puberty was defined in the introduction to

Figure 10 - Comparison of body weights of hand-raised and mother-raised fawns at different ages (1973 - 1976).

Animals who survived until the breeding season and had the opportunity to mate. Not included: 1975 fawns on protein reduced diet.

Graphic symbols for mean, range and S.D. as in Figure 7.


BODY WEIGHT (in kg.)
35
30
25
20
15
10
5
AGE (in days)
25
75
125
175
n = 25
n = 14
n = 25
n = 14
n = 22
n = 9
n = 22
n = 9
a
b
a: Hand-raised Fawns
b: Mother-raised Fawns

this thesis as "the period of life at which reproduction becomes first possible", and not — "at which reproduction actually occurs". In female black-tailed deer the periods of life described by these definitions coincide under normal circumstances, i.e. when healthy fertile males and females have access to each other during the breeding season. However, the term "reproduction" in females includes the occurrence of ovulation, successful copulation, the fertilization of ova, the implantation of the fertilized ova, and the birth of viable offspring. If the completion of the reproductive process, i.e. birth, is used to determine reproductive success, it is possible that some female fawns may have started the reproductive process without this being detected. They could have either, A. ovulated but not conceived, or, B. ovulated and conceived but lost the zygote before implantation or, C. initiated post-implantation pregnancy but lost the embryo by resorption or abortion.

The occurrence of A. is possible, as Thomas (1970) found that a high percentage of first ovulations in adult black-tailed deer was accompanied by silent heats, so that these females did not mate and the ova were not fertilized. However, subsequent estrous cycles normally led to fertilization. A. and/or B. occurred in about 4% of N. W. Bay black-tailed deer (Thomas, 1970), while this pre-implantation loss was 5.1% in Washington State black-tailed deer (Brown, 1961), 6% in California black-tailed deer (Taber, 1953) and 7.5% in Utah mule deer (Robinette _et al._, 1955). Possibility C., the loss of embryos after the implantation stage, was found in 4.3% of N. W. Bay black-tailed deer

(Thomas, 1970), in 6.9% of Washington State black-tailed deer (Brown, 1961) and in 8.8% of Utah mule deer (Robinette et al., 1955).

All the previous observations were made in adult deer but not in fawns. While ovulation does occur in wild fawns, as shown by Thomas' (1970) observation that "large and ruptured follicles are common in wild fawns during the breeding season" (p. 134), this does by no means indicate that a completed pregnancy will result.

In wild populations only 3 black-tailed deer giving birth as yearlings have ever been reported (Shantz, 1943; Thomas and Smith, 1973). There is evidence that an absence of parturition in wild yearlings is not caused by post-implantation loss of the embryo, as the reproductive tracts of a large number of examined fawns showed no signs of pregnancy, (Thomas, 1970; Jordan and Vohs, 1976). It is not known whether the wild fawns that ovulate undergo a silent heat with ovulation but without mating, and do not ovulate again, or whether they do actually mate but the fertilized or non-fertilized ova are lost before implantation, as corpora lutea rarely develop in wild fawns (Thomas, 1970). However the second possibility does exist in captive fawns, as indicated by the fact that in this study matings with a fertile buck were observed in 6 female fawns during the 1973 breeding season, but none of these matings resulted in pregnancy. Although 4 of the fawns that had been observed copulating (intromission and ejaculation occurred) did conceive at later, unobserved matings, the remaining 2 did not give birth in 1974 (possibility of fetuses being resorbed). Observed matings cannot, therefore, be taken as evidence that reproduction is possible, but the production of viable offspring is irrefutable evidence of reproduction.

The results of this study indicate that captive fawns under specific experimental conditions respond reproductively like wild yearlings, i.e. some individuals ovulate, conceive and subsequently give birth. It is, therefore, possible that the finding of ovulations that do not result in pregnancies (Thomas, 1970) in wild fawns is not entirely relevant to captive situations. That post-implantation losses can occur in captive fawns was shown by the death and resorption of the fetus in a pregnant fawn (Figure 11).

Using the subsequent production of offspring as a criterion, during the 1973 mating season, 13 of 20 female fawns became pregnant. All these fawns were wild caught and hand-raised. This included 3 Washington State fawns (#29, 30, 31) originating from a population with larger morphological measurements than the Kelsey Bay population, and 4 Kelsey Bay fawns (#3, 5, 8, 22) for whom insufficient growth data had been collected and who, therefore, had not been included in growth comparisons. The quantitative restriction of feed (to 70% of the intake of the last week before start of experiment) during 48 days of late growth had no influence on weight increase (Table XVII). In comparison to an ad libitum diet it also had no negative influence on the attainment of precocious puberty. Considering only the fawns used for the growth comparisons, it was found that 5 of 6 of the low weight (feed-restricted) animals and 4 of 7 of the high weight (non-restricted) animals became pregnant (Table XVII). If the breeding

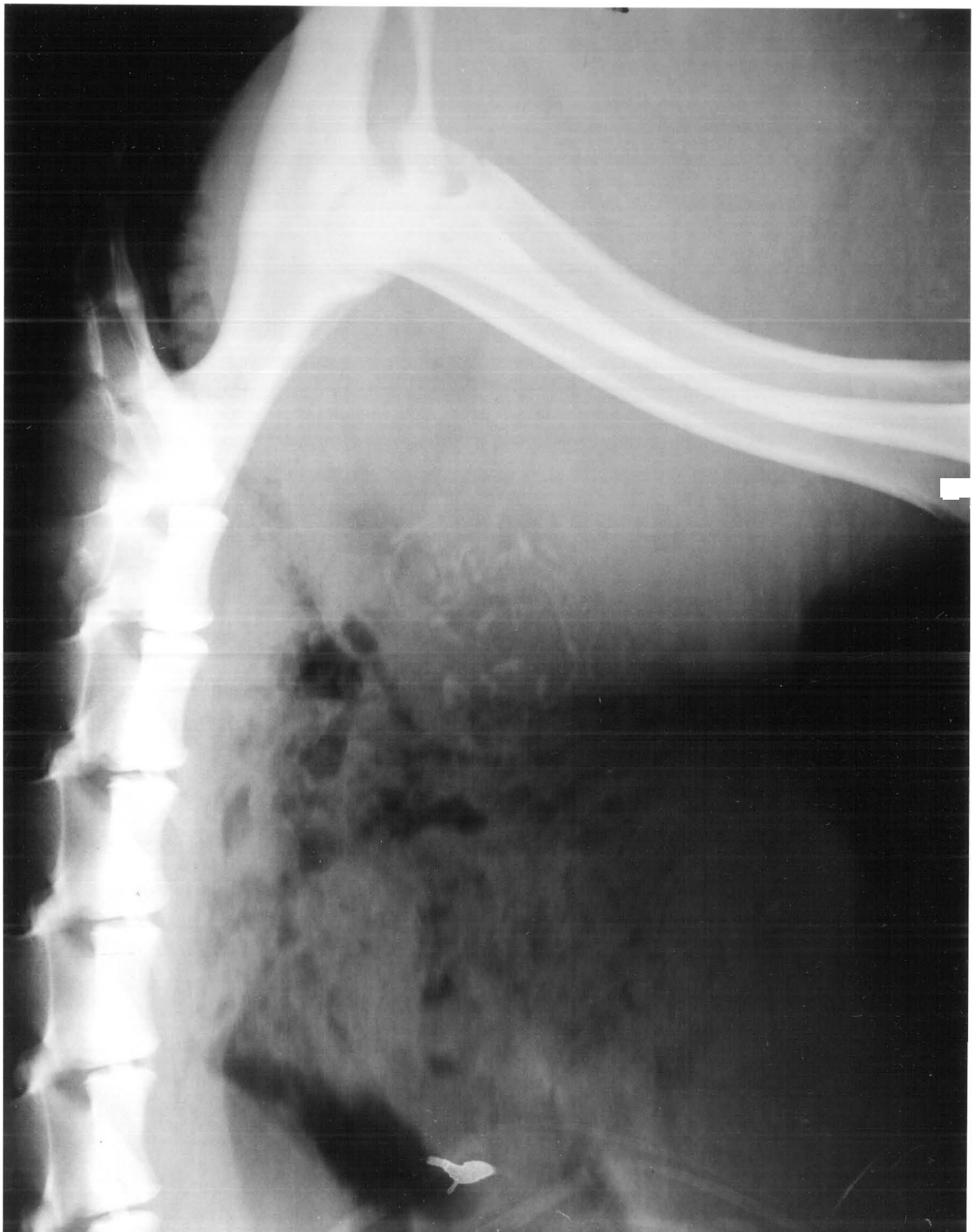
Figure 11 - X-ray photographs of pregnant fawns.

A. Live fetus, March 28th, 1977 (#23-E)

B. Dead fetus, March 28th, 1977 (#31-B)

C. Resorption almost completed, April 13th, 1977 (#31-B)

A.



B.

C.

success of <u>all</u> 20 normally developed female fawns is considered (including those with insufficient weight data, see above), the result becomes 5 pregnancies in 6 low weight (feed-restricted) fawns and 8 pregnancies in 14 high weight (non-restricted) fawns.

The proportions of conceiving and non-conceiving fawns in the low weight and the high weight group are not significantly different ($x^2 = 0.372$). The wide range (October 24th - January 17th) and the late mean (December 21st) of conception dates in precocious fawns in 1973 (Figure 5) can be attributed to the husbandry regime used. Ten of the conceivers and 7 non-conceivers were kept from October 28th until December 18th in small, individual pens and mated under observation with a buck who was introduced daily for a short time. Blood samples (which were subsequently not used in this study) were also taken at regular intervals. Only 1 fawn conceived under these conditions (#14: December 2nd). It is possible that the stress resulting from this type of maintenance was responsible for the delay of precocious puberty in most fawns in 1973 as this phenomenon was not observed in subsequent breeding seasons (Figure 5). There can be no doubt that some stress did occur as the daily introduction of the buck into a small enclosure, without escape routes to permit his avoidance by the does, caused visible anxiety of the latter. Some stress was probably also induced by the blood-sampling procedure twice a week as the animals had to be immobilized with succinylcholine (Anectine, Burroughs Wellcome; 0.06 - 0.115 mg/kg i.m.), a drug which does not affect consciousness but causes temporary paralysis of the motoric muscles. That stress can delay puberty through increase in adrenal steroids, or decrease fertility after puberty has been achieved, has been shown in work on rats by Christian (1960, 1961) and Hagino (1968). An increase of steroids in the blood (thought to be of adrenal origin) after immobilization with succinylcholine was found by Wesson et al. (1976) in white-tailed deer.

During the 1974 mating season all yearlings who had bred as fawns bred again, proving that precocious pregnancy does not impair later reproductive success. Also all 7 animals who had presumably not attained puberty as fawns, as they did not produce offspring, did breed as yearlings. Of the 7 female fawns born to yearlings in 1974, all of which were left with their dams, 3 lived to the breeding season, but 2 were not properly developed (#5-A: coccidiosis, #21-A: partial lactation failure of dam) and therefore only 1 (#22-A) could be used for this study. Another mother-raised fawn that was available in 1974 (#0-B) had been born to an adult doe. In addition there were 5 wild caught hand-raised fawns (#E, G, I, J, K).

Three of this total of 7 fawns produced offspring in 1975 and had therefore conceived in 1974.

As in 1973 stress also occurred during the 1974 mating season. It was caused by the harassment of the deer herd by dogs, which, on one occasion, even broke into the paddock and killed a male fawn (#L, January 23rd, 1975).

During the mating season of 1975, 7 mother-raised fawns and 5 hand-raised fawns were used in breeding studies. As mentioned earlier (Table XII), 2 of the mother-raised (#5-C, 19-A) and 3 of the hand-raised fawns (#3-C, 23-C, I-B) were put·on a protein-reduced diet. Also added to this group was a mother-raised fawn (#31-A) of Washington State stock that had not been used in growth comparisons. Two of the mother-raised fawns in the high-protein group (#17-C, 18-A) were killed by dogs before and during the mating season, leaving 2 mother-raised (#16-B, 22-C) and 2 hand-raised fawns (#16-C, 17-B) in this group. Of 10 female fawns thus left to survive until after the 1975 mating season (3 low protein, mother-raised; 3 low protein, hand-raised; 2 high protein, mother-raised; 2 high protein, hand-raised) only 1 conceived and gave birth in 1976. This animal had been hand-raised and was 1 of 4 on a high-protein diet (#16-C). As mentioned earlier, it was surmised that none of 6 fawns on a low protein diet attained puberty as none of them gave birth. However, the possibility of fetus resorption does exist.

As it was not possible to compare this proportion with that of fawns on the high protein diet by means of the usual χ^2 test, the significance of this result was tested by a one-tailed binomial test (Zar, 1974) using a null hypothesis of a 50% probability of breeding. Since $p\ (X \geq 0) = 0.0156$, which is less than 0.05, H_0 was rejected. Thus significantly fewer fawns bred under conditions of decreasing protein than on a consistently high protein diet when all fawns on high protein diets during the course of this study (of which approximately 50% bred) are considered as the control group. This seems justified in view of the small sample sizes and the similarity in the maintenance conditions over the 4 year period of this study.

It should be mentioned that, as in 1974, during the breeding season of 1975 there was repeated harassment of the deer herd by dogs which approached the enclosure at night in packs, barked, ran about and no doubt caused great stress mainly to the high-protein deer. These animals were kept in the area of the enclosure which was also used as a trap and were, therefore, most vulnerable (Figure 1). In 2 cases the dogs broke into the enclosure of the high-protein group and killed 2 fawns, as mentioned earlier (Table XII). It is impossible to say to what degree this stress delayed puberty beyond the point where increase in daylight hours prevented its occurence. However, Gavitt et al. (1975) found that harassment by dogs during pregnancy (October-April) had no detrimental effect on the reproduction of an enclosed, dense population of white-tailed deer (O. virginianus). Also, in this study, the low-protein fawns (none of which attained puberty) suffered little from dog harassment as they were able to seek refuge in the densely treed area of the enclosure (Figure 1).

The result of the 1975 mating season should also be viewed in relation to the possible effect of estrogenic compounds (e.g. coumestrol) in the diet. The presence of such phytoestrogens in fresh and dried alfalfa was demonstrated by Pieterse and Andrews (1956) in experiments on mice. They found spring crops to contain more estrogenic activity than later crops and leaves more than stems. Although estrogenic activity was found by these researchers to vary considerably within the same plant species and to be affected by differences in season, stage of growth and other environmental factors (such as locality), it is theoretically possible that the captive deer used in this study ingested considerable quantities of estrogenic compounds as their diet contained large quantities of alfalfa hay. This hay was always of 3rd or 4th crops (and, therefore, contained perhaps only small amounts of estrogenic substances) but the deer ate only the leaves and the terminal, thin parts of the stems (and, therefore, those parts containing potentially most estrogenic activity).

Bickoff (1968) stated that phytoestrogens can sometimes initiate estrus in immature animals and in other cases interfere with normal reproduction. However, the studies reviewed by him showed unequivocally a detrimental effect of phytoestrogens on reproduction. But if indeed estrus can be initiated in immature animals by these substances, this must not be confused with puberty. If estrus is elicited by exogenous compounds, this does not mean that reproduction is possible. Also, it is important to note that before and during the mating season of 1975 all animals on a protein-reduced diet (September 4th, 1975 - March 22nd, 1976) had no access to alfalfa hay. In addition, the alfalfa meal in the pellet ration was reduced from 60 lbs/ton in the 20% protein ration fed to the high protein group to 30 lbs/ton in the 15% protein ration (September 4th - September 24th) and totally eliminated in the rations fed to the low protein group from September 24th to March 22nd. None of the low protein fawns bred, which means that only fawns kept continually on diets containing alfalfa attained puberty. Therefore, it cannot be totally discounted that phytoestrogens contained in alfalfa hay contributed to the sexual precocity observed in this study. However, it is the author's opinion that phytoestrogens did not play a role in the attainment of puberty in fawns, as no detrimental effect on the fertility of yearlings and adult does (the typical effect of phytoestrogens) was observed in any year of this study: all of them gave birth if they had the opportunity to mate. (1973: 1 adult; 1974: 1 adult, 20 yearlings; 1975: 18 adults, 6 yearlings). Furthermore, when a sample of those parts that are eaten by deer (leaves and small stems) of the alfalfa hay used during the 1976 mating season was analyzed (Newsome, pers. comm., 1977) it was found to contain only 15 ppm coumestrol. It is not likely that this extremely small amount of phytoestrogen had any influence on puberty attainment. Alfalfa was found to contain from 1 to 400 ppm coumestrol by Hansen et al. (1965).

In 1976 12 mother-raised female fawns were in the experimental enclosure during the rut, but 5 of them were shipped out in late winter in order to reduce the size of the experimental herd. Of the remaining 7 fawns 5 became pregnant. As this manuscript was completed before the 1977 fawning season, attainment of puberty was not determined by the occurrence of parturition but of pregnancy which was established by x-raying these animals on March 28th. Pregnancy was determined by inspection of x-ray photographs which, in 5 cases, showed clearly the presence of a single fetus. This was the highest percentage of precocious pregnancies recorded for 1 year during the 4 years of observation. It was also the first observation (other than a single case: #0-B) of mother-raised fawns conceiving in the year of birth. It is interesting that in 1976 stress before and during the breeding season was minimal compared with previous years, as no experimental, potentially stress-inducing situation existed, and the dog problem had been eliminated. However, in 1 fawn (#31-B) the x-ray photograph on March 28th showed a fetal skeleton which, because of its blurred contours and the abnormal position of the fetal bones, was considered to be that of a dead fetus. When the same animal was x-rayed again, 16 days later, only few, unclear remains of bones could be seen (Figure 11). There is no doubt that the fetus had died at about the middle of the pregnancy, and that the fetal tissues were subsequently resorbed.

To summarize the above results, 22 of 44 fawns (50%) who had the opportunity to breed and whose subsequent reproductive history was known bred during their first breeding season i.e. at approximately 6 1/2 months (min. 142 days, max. 253 days) of age from 1973 to 1976. If data from the 1975 experiment on lowered protein levels are deleted, 21 of 34 fawns (62%) bred. If data from the 1976 season are also deleted because pregnancy had not been determined by the occurrence of parturition but by the presence of fetuses of which at least one was not carried to term, the ratio changes to 16 of 27 (59%).

It is appropriate at this point to compare the sizes of wild fawns during the first November-December and those of yearlings during the second November-December of their lives with the sizes of captive fawns in this study. In 12 years, from 1954 to 1965, 314 female fawns and 276 female long yearlings were killed by hunters during the hunting season (November 6th - December 6th) at North West Bay on Vancouver Island. The dead weights (carcasses eviscerated) were recorded and kindly provided for this study by the Nanaimo office of the Fish and Wildlife Branch of British Columbia. These weights were converted to total (bled) body weights by use of a regression formula ($r^2 = 0.987$) calculated by A. Anderson (Wildlife Research Centre, Fort Collins, Colorado) for 56 mule deer (O. h. hemionus) under 17 months of age (Appendix B). This formula is $y = 0.0602 + 1.3714\ x$ (where y = bled weight in kg and x = eviscerated weight in kg). The exact relation between bled weight and live weight is unknown, as the amount of blood lost by an animal killed by a gunshot and bled later by slashing its throat can vary to a large extent. However, as the total amount of blood in domestic sheep was found to be 1/12 of the body weight (Miller and West, 1967), it is not likely that in deer the bled weight differs by more than that amount from the live weight.

In 1975, between January 22nd and January 25th, 6 wild female fawns were killed for this study in the Adam and Eve river valleys near Kelsey Bay on Vancouver Island, -- the same area where the original breeding stock for the experimental herd had been collected. These animals were weighed immediately after death and their weights were recorded. None of them were pregnant and no corpora albicantia, corpora lutea or Graafian follicles were found in their ovaries.

The values for the wild fawns and long yearlings from North West Bay and the wild fawns from Kelsey Bay are presented in a graphic comparison with the experimental animals. As noted earlier (Figure 7), the experimental animals who conceived as fawns and gave birth as yearlings were significantly heavier at 125, 175 and 225 days than those who did not. Although it could be argued that the weight difference at 225 days of age was due to physiological changes caused by the initiation of pregnancy (most precocious animals conceived before reaching this age), the significant weight difference between the 2 groups at 125 and 175 days cannot be disputed. The range of weights (max.: 34.9 kg) of wild N. W. Bay fawns killed between 170 and 175 days* of age overlapped the range of precocious (min.: 24.0 kg) and non-precocious experimental fawns (min.: 21.8 kg). This, however, is perhaps somewhat misleading (Figure 12). Some of these high values within the range of weights can almost certainly be attributed to errors of age estimation under field conditions as some of them equaled weights of 1 1/2 year old does from the same area. Normally, all black-tailed deer have fully developed, permanent first incisors at 15 - 18 months of age and a complete set of permanent incisors at 20 - 21 months (Brown, 1961). Therefore, yearlings of this age are usually not mistaken for fawns if they have changed teeth at the normal time. But Robinette _et al._ (1957) found four to ten months variation in the age of mule deer at the time of replacement for most teeth. It is, therefore, possible that some long yearlings had not yet replaced their fawn dentition when shot and were counted as fawns.

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*The weights of the N. W. Bay fawns over a period of 5 days rather than the weight at 175 days of age were used for comparison in order to eliminate the variation between daily samples.

Figure 12 - Comparison of body weights of wild and experimental fawns of different ages during the mating season.

Experimental Fawns (1973 - 1975)

Age: Known age or age calculated from weight at capture ($y=2.29+0.168x$, where y = weight at capture in kg and x = age in days.

Weight: Measured

Wild Fawns and Yearlings, North West Bay (1954 - 1965)

Age: Calculated from mean date of birth at N. W. Bay = June 14th (Thomas, 1970): November 6th = 145 days or 510 days, respectively.

Weight: Calculated from eviscerated weight ($y= .0602 + 1,3714x$, where y = bled weight in kg and x = eviscerated weight in kg; Anderson, pers. comm.)

Wild Fawns, Kelsey Bay (1975)

Age: Calculated from mean date of birth at Kelsey Bay = June 9th (this study): January 22nd = 227 days.

Weight: Total weight immediately after death, measured.

Graphic symbols for mean, range and S.D. as in Figure 7.

The mean weight of the precocious experimental fawns was significantly higher ($t = 5.03$, 105 d.f., $P < 0.01$) than that of the wild N. W. Bay fawns between 170 and 175 days of age ($\bar{x} = 23.1$, S.D. = 3.35, n = 92). The mean weight of the non-precocious experimental fawns was also significantly higher than that of the wild N. W. Bay fawns between 170 and 175 days of age ($t = 3.85$, 103 d.f., $P < 0.01$). But compared to the wild N. W. Bay long yearlings at 540 days of age the precocious experimental fawns were very significantly lighter at 175 days of age ($t = 6.59$, 16 d.f., $P < 0.01$) and so were the non-precocious experimental fawns ($t = 6.39$, 11 d.f., $P < 0.01$).

At 225 days the range of weights of precocious experimental fawns (min.: 25.9 kg) did just overlap the range of wild Kelsey Bay fawns killed between the age of 227 and 230 days (max.: 25.9 kg), but the mean weight of the former was significantly higher than that of the latter ($t = 5.44$, 18 d.f., $P < 0.01$). The mean weight of the non-precocious fawns at 225 days of age was also significantly higher than that of the wild Kelsey Bay fawns between 227 and 230 days of age ($t = 2.99$, 17 d.f., $P < 0.01$), although their ranges of weight did overlap.

In summarizing these findings, it may be said that in late fall and early winter, at the time when most precocious conceptions occurred, the fawns attaining precocious puberty reach a higher average weight than the non-precocious captive and the wild fawns. Although there was a considerable overlap in weights of precocious and non-precocious captive fawns, the overlap was much less between non-precocious captive and wild fawns and only minimal — if existent (see previous discussion of fawn aging in this section) — between precocious captive and wild fawns.

GENERAL DISCUSSION AND CONCLUSIONS

One of the major problems of experimental work with large wild mammals is the restriction to small sample sizes. This results from the difficulties and costs of collecting breeding stock from the wild and of subsequent housing and maintenance of the experimental animals. In addition, sample sizes are necessarily small when one is working on the reproduction of a seasonally breeding species with only 1 birth per year and with litters of 1 or 2 young. The results obtained in such studies may not, in many cases, offer statistically significant data and thus can sometimes only be taken as an indication of phenomena and processes involved. All this, of course, applies to a study on reproduction in deer.

In spite of this restrictive statement, question number 1. asked at the beginning of this study, namely whether breeding in female black-tailed deer under 1 year of age occurs only in rare cases of reproductively anomalous animals or regularly under certain conditions of captivity, has been clearly answered. Precocious puberty occurred in everyone of the 4 years of study: 1973 in 13 of 20 (65%) of all normally developed, healthy female fawns, 1974 in 3 of 7 (45%) and 1976 in 5 of 7 (71%). In 1975, when only 4 fawns were kept on the same high protein diet as in the other 3 years of this study, puberty was attained by 1 of these 4 (25%). No negative effect of precocious puberty on subsequent reproduction was seen for up to 3 years afterwards. All precocious does who survived and had access to bucks produced healthy twins as 2 year olds and, in the case of the 1973 animals, as 3 year olds. The birth weights of the fawns born to yearlings which conceived as fawns equalled and surpassed that of fawns born to older does (Table XIII). Although the sample sizes were rather small, it appeared that precocious females remained lighter than the non-precocious ones (Table XIII), presumably due to growth retardation by early pregnancy and lactation. It is not known whether this weight difference disappears later in life. Two questions followed:

2. Is the shortening of the time necessary to reach puberty by at least half (attainment of puberty in precocious captive black-tailed deer at 1/2 year of age, in wild ones at 1 1/2 years of age or older) in the female fawns caused by nutritional factors?
3. If it is caused by nutritional factors, is this reflected in the achieved weights?

Although black-tailed deer fawns do not normally breed in the wild, it is known that a percentage of yearlings reaches puberty and that this percentage is influenced by range conditions (Taber, 1953: Taber and Dasmann, 1957, 1958; Cowan, 1956). In white-tailed deer, where wild fawns frequently attain puberty (Table II), it was observed that good range conditions increase the percentage of breeders (Cheatum and Morton, 1946; Cheatum and Severinghaus, 1950). However, it must be realized that range quality is usually not measured in terms of the actual amount of digestible nutrients that are available to deer in a certain area, but rather by indirect indicators such as the browse species present, topography, climate and soil quality. These factors are then correlated *a posteriori* to the fertility and fecundity of the deer populations present (Cheatum and Severinghaus, 1950).

In many cases the stated observation that a range is of good quality and that on this range the deer have a high reproductive rate cannot be taken as irrefutable evidence that nutritional factors influence reproduction, as the range was probably classified as "good" by the observation of a high reproductive rate of the deer in the first place (Taber, 1953). However, experimental work on nutrition in penned white-tailed deer showed conclusively that productivity and puberty attainment is related to nutrition: on quantitatively inadequate rations 6 of 13 female yearlings did not breed and fawn production of yearlings and adults was reduced (Verme, 1969). The latter result was also obtained by protein reduction (Murphy and Coates, 1966).

It is most likely that the acceleration of puberty observed in this study was also due largely to nutritional factors. There was a considerable difference in feed protein content and digestibility (references see page 94) between the feed of captive fawns on high protein diets and wild fawns on late fall forage. Other environmental factors, such as light and temperature, were not altered in comparison to conditions in the wild. The research enclosure in Maple Ridge was situated well within the limits of the natural distribution of black-tailed deer (Alaska to California), and the captive deer were subject to the same climatic conditions as wild deer. The only other factors, apart from nutrition, that had been altered were space and thus degree of social contact and, perhaps, activity. The 1 hectare research enclosure contained from 32 to over 50 deer at any given time during the 4 years of study. This density was many times greater than in free-ranging black-tailed deer which occupy individual home ranges with a maximum diameter of 640 - 1,280m and during the fawning season territories which are separated by at least 137m (Dasmann and Taber, 1956). It is conceivable that this high density could have caused stress which is known to delay puberty (Christian, 1960, 1961; Hagino, 1968) through the release of adrenal corticosteroids. However, in this study an acceleration of puberty was observed in comparison to wild deer. It is possible, however, that stress may have delayed early puberty in certain cases. This delay could have been sufficient for the increase in daylight hours to prevent the occurrence of puberty altogether for that breeding season. In certain "short-day" breeding species puberty can only be attained when the day length has decreased to a certain critical level (e.g. domestic sheep, Hammond Jr., 1944; Hafez, 1952), and this has also been postulated for black-tailed deer (Linsdale and Tomich, 1953).

While theoretically the possibility exists that the restriction of living space may have delayed puberty through stress due to the intensification of social interactions (although no evidence was found for this presumption), it also may have contributed to the acceleration of puberty due to an energy-saving decrease in activity.

The nutrition of the captive deer remained equally high throughout the year, but the nutritional value of the forage of wild deer is known to change drastically from a maximum in late spring to a minimum in late winter as deduced from the annual change in crude protein content throughout the range of the species (Vancouver Island: Gates, 1968, Rochelle, pers. comm., 1976; Oregon: Einarsen, 1946; California: Bissell and Strong, 1955; Colorado: Dietz et al., 1958). As a rule, the protein content of plants is highest during the growing period and lowest during the dormant period (Hellmers, 1940). On Vancouver Island the protein content changed from an average maximum of 17% - 19% to an average minimum of 6%. In addition the digestibility of crude protein in browse plants during the winter was found to range from 10.7% to 48.5% in digestion experiments on mule deer in Utah (Smith, 1957) as compared to 78.5% in alfalfa, 86.5% in oats and 88.4% in barley fed to cattle (Morrison, 1948).

It is thus clear, from the above observations, that the level of protein nutrition generally available in fall and winter to wild deer is considerably different to the level of protein nutrition available to experimental deer in this study (Table VII). However, this does not necessarily mean that the same difference existed in the amount of protein that was actually assimilated, as rumen microbes can synthesize protein from non-protein nitrogen compounds. It is insufficiently known to what degree this can counterbalance differences in feed protein content.

Some light was shed on this problem by Bissell's (1959) discovery that the rumen contents of black-tailed deer eating natural browse in California contained 2 to 3 times as much protein as had been calculated from forage plant analyses (6% - 7%). But Bissell's (ibidem) results can be criticized on at least 2 grounds, both of which would decrease the difference between forage and rumen protein: A. The theoretical protein contents of the rumens were based on vegetation analyses which did not take into account selective feeding on plant parts with high protein content. B. The protein contents of the rumens were calculated from the total rumen nitrogen contents. Thus the nitrogen content of urea and other non-protein nitrogen compounds was included in the analysis. But these compounds can only be utilized for protein synthesis to a certain degree by rumen microbes. Blackburn (1964) has noted that only a maximum of 50% of diet protein can be replaced by these compounds. Therefore, Bissell's calculation of protein from rumen nitrogen could be a considerable over-estimation. Bissell (*ibidem*) found only a slight difference between the protein percentage of alfalfa pellets and that of the rumen content of deer who had been fed exclusively on these pellets. One has to draw the conclusion that the difference in deer on a browse diet is due either to urea recycling through saliva, which is increased at low protein diets (Kay, 1963) and/or urine ingestion (Smith *et al*., 1975), or to the selective feeding behaviour of the deer. The latter explanation is endorsed by Brown (1961) who found in feeding experiments on black-tailed deer with natural browse that the nutritive value of many species during the winter was so low as to cause severe weight losses and, in some cases, even death in the experimental animals which did not have the opportunity to feed selectively. Trailing blackberry (*Rubus ursinus*, Chamisso and Schlecht), which contained the highest percentage of protein (average 10.63%), was the only natural browse species on which deer were able to maintain their body weight. According to Einarsen (1946), black-tailed deer are not able to survive on diets containing less than 5% protein which is similar to the minimal protein requirement of white-tailed deer, suggested by McEwen et al. (1957) to be 7 - 9%.

Although protein is greatly reduced in the winter forage of wild deer, this reduction is not balanced by an increase in other nutrients. Dietz et al. (1958) found in 5 key browse plants of mule deer in Colorado that the easily digestible carbohydrates decreased slightly in the winter (N-free extract from 58.44% to 57.84%) while relatively indigestible carbohydrates increased (crude fiber from 19.69% to 23.88%). Crude fat was found to increase slightly (from 4.9% to 5.25%), however, it should be pointed out that crude fat is a poor measure of food quality as it includes soluble compounds such as resins and waxes which are of little or no nutritive value. Abell and Gilbert (1974) have noted that "adequate levels of crude protein in the diet of deer affect positively other important nutritional aspects [such as] digestible energy, digestibility of non-protein constituents and maintenance of a healthy population of rumen microbes" (p. 522). Fiber content, on the other hand, is negatively correlated with digestibility and food intake.

In an experiment on roe deer being fed natural browse throughout the year, Drozdz and Osiecki (1973) found that a) the digestibility of dry matter decreased from 87% in May to 34% in January and the food intake decreased from 600g dry matter in summer to 350g dry matter in winter, and b) the crude fiber content increased from 13.9% in May to 40.7% in January and the crude protein content decreased from 19.8% in May to 8.0% in January. This indicates that these deer did not counteract the deterioration of the nutritive value of natural forage by an increase in consumption.

It was also found in the study by Dietz et al. (1958) that carotene* decreased from 85.89 in the summer to 17.81 micrograms per gram in the winter. The rations of the captive deer in this study always contained 3,300 I.U. vitamin A per kilogram.

As would be expected, the superior nutrition of the captive fawns during late fall and winter resulted in higher weights due to their continued (albeit slow) growth when compared to wild fawns at the same time of the year (Figure 12), although restricted movement causing a decrease in energy expenditure may have been a contributing factor. It was shown in experiments on white-tailed deer fawns that a feed ration with high (Ullrey et al., 1967: 20.2%; Kirkpatrick et al., 1975: 18.2%) crude protein levels did indeed produce significantly higher weight gains than rations with low (Ullrey et al., 1967: 12.7% and 7.8%; Kirkpatrick et al., 1975: 9.6%) levels. It is not likely that wild fawns grow differently from captive fawns during the early period of their lives, as their feed and that of the nursing dams is, at that time, abundant in quantity and equal in quality to the feed of the experimental deer (Gates, 1968; Rochelle, pers. comm., 1976).

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*Carotene is changed by the body into vitamin A which is important for reproduction.

The growth of wild fawns stagnates during the time of year when nutrition is low and energy loss is high. In the captive fawns, growth continued during the winter but at a rate lower than that during the summer. This reduction of the growth rate was probably due to lower metabolism. It cannot be attributed to attainment of puberty as it occurred in all fawns, precocious and non-precocious. Metabolism is generally lower in deer during the winter as was indicated by a lower fasting metabolic rate during the winter in experiments on white-tailed deer (Silver et al., 1969, 1971; Thompson et al., 1973). The lower energy demand leads to voluntary restriction of feed consumption (black-tailed deer: Bandy, 1955; white-tailed deer: French et al., 1960; Long et al., 1965; Behrend, 1966; Fowler et al., 1967; Ullrey et al., 1967; Thompson et al., 1973, Kirkpatrick et al., 1975).

If attained weight is a decisive factor in the attainment of puberty in black-tailed deer, a weight difference during the mating season not only between the captive and the wild fawns but also between the precocious and the non-precocious captive fawns should have been apparent. This was indeed shown by comparisons of weights of precocious and non-precocious captive fawns at 125, 175 and 225 days of age and by comparison of the weights of these fawns with those of wild fawns during the mating season. It is important that only weights of animals of the same population were compared since local populations of black-tailed deer in different environments reach very different ultimate body size (Cowan and Wood, 1955; Bandy, 1955).

As the observed weight differences between precocious and non-precocious experimental fawns did not exist in early life (at 25 and 75 days) when most of the fawns' nutrition was supplied by milk, it is likely that it was caused by a differential intake of nutrients (e.g. difference in beginning and degree of voluntary restriction of consumption) after weaning. This is also indicated by the fact that the growth patterns of precocious and non-precocious fawns in early life (to inflection point) were identical (Table XV). However, the possibility exists that differences in digestive or metabolic efficiency played a role in the achievement of differential weights.

The comparison of the weights at the end of the breeding season as percentage of the adult weights of both groups yielded essentially the same result as the comparison of absolute weights: the precocious fawns were significantly heavier (Table XVI). However, this is probably due, at least in part, to the fact that their adult weights are lower (Table XIII).

Comparisons of captive (precocious <u>and</u> non-precocious) and wild fawns showed a significant weight difference at 175 and 225 days. Weights at early ages could not be compared as wild fawn weights were not available for animals under 145 days of age. But, as stated before, it is not likely that wild fawns grow differently from captive fawns during the early part of their lives. However, their birth weights might be different due to a difference in the nutrition of the dam during pregnancy.

Although the weights of precocious fawns were significantly higher during the mating season than the weights of non-precocious fawns (captive and wild), the fact that the weights of all 3 groups showed considerable overlap (Figure 12) precludes the possibility of a simple threshold effect of weight on puberty attainment. Rather, it indicates that the critical weight of the population is represented by a range within which each animal has its own individual critical weight. For example, one fawn may not have reached its individual critical weight at 25 kg while another one has reached it already at 22 kg.

That weight per se is a good indicator of the state of somatic development and thus related to the attainment of puberty, was not only shown by this study but also by work on other mammals (see references in "Results and Discussion", section C. Growth). The conclusions reached were identical: puberty can only be attained above a certain species-specific critical weight (represented by a range), at whatever age this critical weight is reached.

The 1973 experiment of a reduction of food intake to 70% (Table XI) for 1 group of fawns, which was expected to result in a reduced weight increase enhancing the lower absolute weights and thus a lower percentage of precocious fawns in the low intake (-low weight) group, did not achieve this result. The low intake group and the control group showed the same weight increase and the percentage of precocious breeders was actually higher in the low intake (-low weight*) group although not significantly so. This result can be explained by the sample size as smaller fawns can sometimes attain puberty earlier than larger ones due to the

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*The lightest fawns had been selected for this group.

previously mentioned range in individual critical weights. As the weight increase was the same for both groups, it was concluded that the control fawns voluntarily restricted their food intake to approximately 70%, and that this amount of food contained sufficient nutrients to allow those fawns that had passed their individual critical weight to attain puberty. If this experiment was to be repeated, the feed intake should be restricted earlier and to a greater degree in order to have the experimental fawns duplicate the growth pattern and the weights of wild fawns in late fall and winter. Also, the food intake of the control group should be measured.

The 1975 experiment of a step-by-step reduction of crude protein (from 20% to 7%) in the feed rations of 6 experimental fawns* did not result in weight gains that were different from those of 4 fawns in a control group whose feed was maintained at a 20% crude protein level. The energy levels of the protein reduced rations were maintained constant and the quantitative food consumption was not restricted. Therefore, it must be concluded that these low protein levels were still sufficient to allow the same growth as in the control animals, due to the high energy content and digestibility of the commercial feed. It is also possible that the low protein animals compensated for the low protein levels to some degree by eating more. As a result, the low protein animals could obtain sufficient energy for maintenance from the non-protein constituents of their rations and had sufficient

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*Of these only 5 were of Kelsey Bay stock and were used in weight gain comparisons.

digestible protein available for growth in spite of the low crude protein levels in the experimental rations. It can be surmised that the high digestibility of the ingredients of the experimental rations provided the low protein experimental deer with amounts of digestible protein that exceeded those in natural browse during the dormant period of the vegetation. This is shown in Figure 13 which is described in greater detail later in the text. Increased consumption and, probably, increased urea recycling in comparison to the high protein group can be assumed to have increased the protein actually available to the low protein group to some degree.

However, there is no reason to believe that this totally eliminated the difference between the 2 groups. The crude protein content in the feed of the high protein group was 2 to 3 times higher than that of the low protein group (Table XII). Although the quantitative feed intake of the two groups was not measured, no dramatic increase in consumption of the low protein group was noticed when the crude protein content of the feed was lowered. Furthermore, Ullrey et al. (1967) did achieve weight differences in white-tailed deer fawns on high and low crude protein diets which were similar to diets in this study although compensatory feeding was possible. Obviously, these fawns had been unable to compensate to any large degree for experimentally prescribed differences in feed (crude) protein. It is logical therefore to assume that the black-tailed deer fawns used in this study did not respond entirely differently. The fact that the black-tailed deer fawns did not show differences in weight gains while the white-tailed deer fawns did can be explained mainly by the white-tailed deer fawns being separated from their dams at the beginning of the experiment and having to depend entirely on the experimental rations. In contrast, the black-tailed deer fawns on the low protein diet in this study were left with their dams until they were naturally weaned at the end of October (3 mother-raised fawns) or weaned from the bottle on October 1st (3 hand-raised fawns). Smith et al. (1975) noted that fawns benefit from nursing prolonged into fall. In addition, the energy loss of the white-tailed deer fawns in the experiment of Ullrey et al. (1967) was much greater, as these workers reported much lower temperatures during their experiment (September 27th - October 10th: average high 16 F, average low 2 F; December 20th - January 3rd: average high - 3 F, average low - 10 F) than those recorded in 1975 for the location where the present experiment was done (Appendix D). It is, therefore, likely that those white-tailed deer had to use a higher proportion of their feed protein for maintenance so that insufficient protein was left for growth. As Ullrey et al. (1967) did not mention the amount of digestible energy per kg of feed, it is also possible that this was less than the digestible energy of the feed of the experimental black-tailed deer in this study (3,167 kcal/kg).

As in this study none of 6 fawns on a low protein diet but a high percentage of 38 fawns on high protein diets (1973 - 1976) attained puberty while the weight gains were not significantly different, it was concluded that more protein is necessary for the attainment of puberty than for maximal growth. The achieved growth of the low protein group was assumed to be maximal because it was equal to the growth of the control group on an *ad libitum* diet of 3,167 kcal/kg digestible energy and 20% crude protein. Bandy (1955) considered feed containing 2,854 kcal/kg digestible energy and 15.4% crude protein adequate for nutrition of black-tailed deer fawns. From the requirements of sheep and cattle, it was infered that a growing ration for mule deer should contain 10% - 12% crude protein (Cowan, 1956). The feed of the control group greatly exceeded these values.

The occurrence of precocious puberty in fawns on high protein but not in those on low protein is in accordance with the findings in mice by Vandenbergh *et al.* (1972) who found young mice to mature significantly later on an 8% than on a 16% or 24% protein diet, and also with the findings of Murphy and Coates (1966) in a small number of adult white-tailed deer, which indicated that production of fawns was reduced by lower levels of protein.

As failure to attain puberty was concluded from failure to give birth (except 1976), fetus resorption could have resulted in classifying some precocious fawns as non-precocious. If this had occurred in the low-protein group it would mean that the conclusion of the protein reduction experiment would have to be altered: instead of a critical protein level postulated to be necessary "for the attainment of puberty" it would have to be postulated to be necessary "for the completion of the first pregnancy". In future work on deer reproduction x-ray tests and the occurrence of parturition should be combined to clarify this.

Kirkpatrick et al. (1975) and Abler et al. (1976) reported on an experiment investigating the influence of energy and protein on growth and puberty attainment in white-tailed deer fawns. Twenty-four fawns were divided into 3 weight groups (heavy, medium, light). Two fawns from each group were then assigned for 20 weeks to 1 of 4 diets: 1. High energy - high protein, 2. high energy - low protein, 3. low energy - high protein, 4. low energy - low protein. It was found that weight gains were significantly greater in fawns on high protein diets, but no significant effect of energy on weight growth was found. However, the low energy - low protein diet produced the smallest weight gain. The digestible energy of the high energy rations (3,052 and 3,075 kcal/kg) was similar to the digestible energy of the rations in this study (3,167 kcal/kg), while high protein was 18.2% and low protein 9.2%, compared to 20% and 15% - 10% - 7% - 10% in this study.

In the previously mentioned study on white-tailed deer the influence of nutrition on puberty attainment was also investigated. It was found that all 6 animals on the high energy - high protein diet and 3 of 5 on the high energy - low protein diet (1 had died) had at least 1 observation of 1.0 ng/ml of progestins (presumed to be indicative of ovulation), but that none of 3 fawns on low energy - high protein (3 fawns had died) and none of 5 fawns on low energy - low protein (1 fawn had died) had such progestin levels. It was concluded by Abler et al. (1976) that protein had no apparent affect on progestin concentrations and attainment of puberty. If this was so, an explanation would have to be found for the apparently opposite finding in this study. However, the author is of the opinion that the conclusion from the white-tailed deer study can be criticized because

1. not pregnancy but the arbitrary value of 1 ng/ml progestins was used as indication for the attainment of puberty,

2. blood samples were taken only at 2 and 4 week intervals and, therefore, most likely at very different stages of the estrous cycle (in black-tailed deer 8-9 day according to Thomas, 1970),

3. only 3 fawns remained in the low energy - high protein diet group which, if the heavier animals had died [Abler _et_ _al_. (1976) do not mention this], could account for the failure of the remaining fawns in this group to attain puberty.

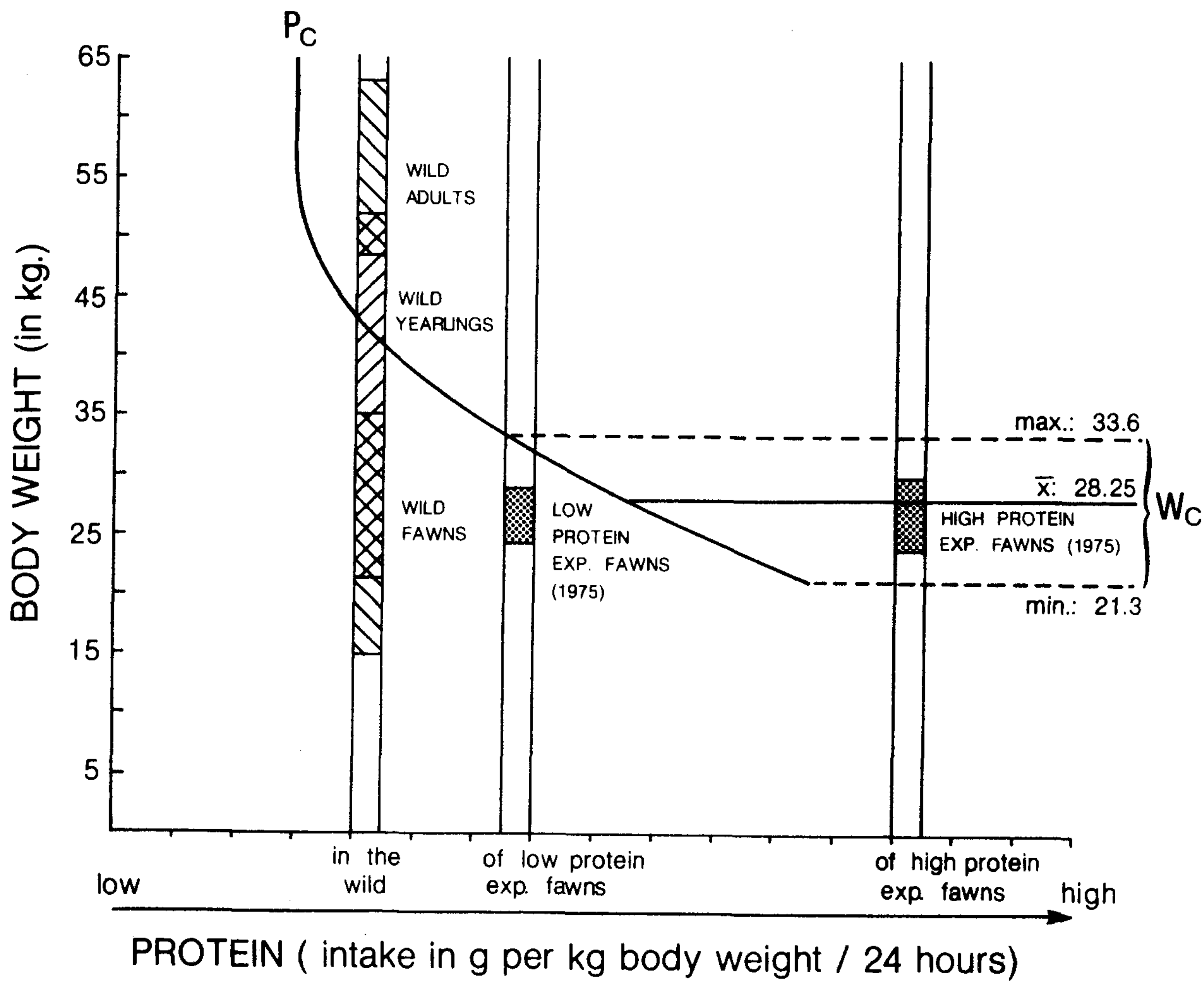
If that experiment were to be repeated with black-tailed deer, it would be advisable to use larger numbers of deer and a direct indication (pregnancy and/or parturition) of puberty attainment. One would then expect to obtain results resembling those of Kirkpatrick's _et_ _al_. (1975) observations on the influence of protein on growth: the high energy - high protein ration having the greatest influence on puberty attainment, the low energy - low protein ration the least influence and the two other rations being intermediate.

As stated earlier, findings in several mammalian species and the significant weight difference between precocious and non-precocious fawns found in this study lead to the conclusion that weight (as an indicator of somatic development) is related to the attainment of puberty, but many wild fawns and wild yearlings achieve weights during the rutting season that equal those of captive precocious fawns (Figure 12) yet they do not breed. Based on the observations of Vandenbergh _et al_. (1972) in mice and the failure of 6 fawns on a low protein diet to attain puberty, it was concluded that a certain, high amount of protein is essential for the attainment of puberty. However, almost all 2 year old wild deer do breed although they forage on the same low protein browse as fawns that do not breed and yearlings of which only a certain percentage breeds.

It is, therefore, suggested that it is an interaction of protein intake and achieved weight which determines whether female black-tailed deer attain puberty (if this interaction results in body weight and protein values above a critical level during the mating season), and that heavier females require less protein during the pre-rutting and rutting season than lighter ones in order to attain puberty (Figure 13). The logic of this suggestion is that after the completion of the rapid phase of growth in early life much less protein is needed for the growth of new tissues and thus becomes available for other processes, including reproduction. Growth has priority over reproduction in the allocation of protein. In addition (and/or alternatively) it is possible that the stimulation threshold of the hypothalamic-hypophyseal-gonadal system is progressively lowered by the progression of the somatic development. This would explain why only a certain percentage of yearlings but almost all does over 2 years of age (except on extremely poor ranges, references see "Introduction") attain puberty.

It was found (Ullrey _et al_., 1967: Kirkpatrick _et al_., 1975)

Figure 13 - Influence of body weight and protein intake on puberty attainment in wild and experimental deer.



P_C: Critical amount of protein during pre-rutting and rutting season (in excess of protein which is necessary for growth)

W_C: Critical weight, range of individual variations

Wild Deer: Approximate weight ranges during rutting season (Brown, 1961; N.W. Bay: F&W Branch)

Experimental Fawns: Weight at end of experiment 1975 (March) that the weight of young deer is directly correlated to feed protein levels, so that protein probably influences the attainment of puberty in 2 ways: indirectly by affecting overall growth, and directly by affecting the function of the endocrine system (pattern of synthesis and/or release of pituitary gonadotrophins and response of the ovary to the latter: Lamming, 1969). The direct effect of nutrition on the endocrine system has long been known in domestic sheep and has been used to increase the ovulation rate through "flushing", i.e. providing the sheep with a sudden burst of feed of high nutritive value prior to mating (Allen and Lamming, 1961; Coop, 1966).

Although the observation made in this study that most fawns conceived later than older females (Figure 5) cannot be considered conclusive (due to the possible delay of puberty by stress in 1973 when most fawn conceptions occurred), the observations on fawns and yearlings of white-tailed, black-tailed and mule deer in the wild indicate clearly that young female deer breed later in the season than adults (references see "Introduction").

As it was found in black-tailed deer that wild fawns and yearlings do not increase in weight during and for some time after the mating season (Figure 12), and as the low quality of forage (energy and protein values) does not improve during that time due to the dormant state of the browse plants, it must be concluded that a third factor is involved in puberty attainment which has higher values at the end of the mating season than at its beginning. This factor is almost certainly the length of the dark period of the day. The seasonality of breeding in black-tailed deer and other northern deer species is a well-known fact (adult black-tailed deer breed in November - December, in exceptional cases breeding is possible until March according to Thomas, 1970), but much less is known about the influence of the photoperiod on the onset of estrus in females than in males (*Cervus elaphus*: Jaczewski, 1954; *Capreolus capreolus*: Bubenik, 1966; 18 species and subspecies: Lau, 1968; *Odocoileus virginianus*: French *et al*., 1960).

That a certain critical length of the dark period of the day is necessary to allow estrus to occur in female deer can be surmised from the season at which estrus has been observed, from the findings in male deer, and by inference from findings in female domestic sheep which also breed in fall. Extensive research in sheep (reviewed by Dyrmundsson, 1973) showed that estrus can only be reached at a certain, short day length. This is also true for the onset of puberty in sheep, but the threshold of stimulation (length of dark period) is greater for lambs than for adult ewes and falls with increasing age (Hammond, 1944). If this is also true for deer, this would explain why young deer breed later in the season than adults. The critical factor is probably not a certain, critical length of the dark period of the day per se but the length of time for which the animals are exposed to days with dark periods above the critical level. This would explain the breeding of young deer at a time after December 21st when the day length is already increasing, although they did not breed at a time with corresponding day length before December 21st.

In this context it is interesting to note that one fawn born in 1974 (#0-B) was remarkable as it was one of the earliest fawns born (May 22nd — only 2 other births occurred earlier in this study) but it was the latest ever to breed (January 30th.) It is tempting to speculate that this animal, had it been born at the time which is normal for the majority of fawns, namely mid-June, would not have reached the individual critical weight necessary to attain puberty before the increase in daylight hours would have shut off the endocrine system that causes puberty if that weight is reached. The extreme data for this particular animal certainly support such a hypothesis.

A visual interpretation of the influence of weight, protein and photoperiod is given in Figure 14. As body weight increases, the critical values of the stimuli (protein and darkness) necessary to elicit puberty are decreasing to a certain point. Below these minimum critical levels does cannot attain puberty no matter how high their body weight.

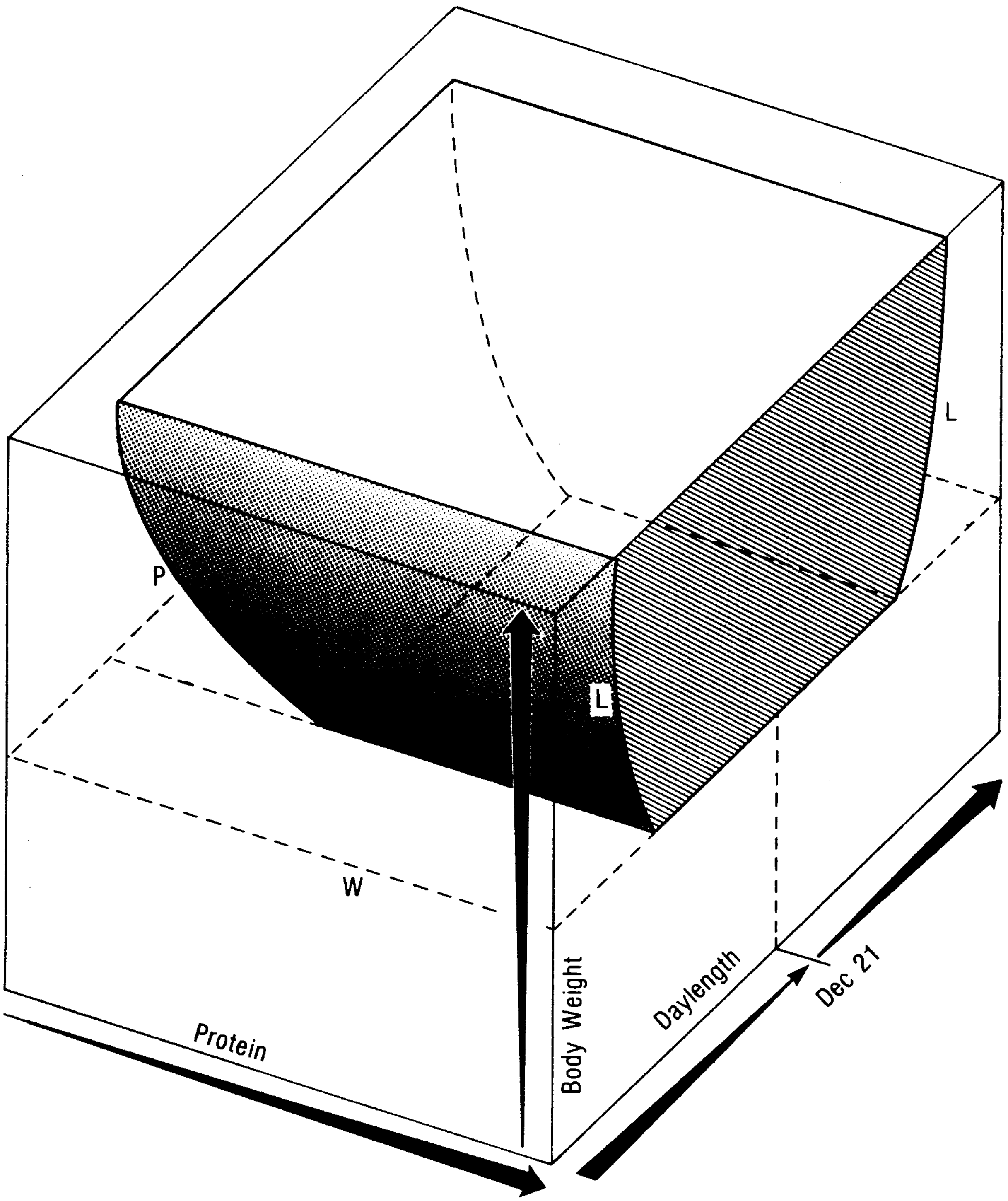
It is still unproven whether a certain daily allotment of protein during a period (the duration and timing of which is unknown) of the pre-rutting and rutting season is necessary in order to stimulate the endocrine system directly as suggested in Figure 13. However, this suggestion is supported by the fact that "proteins or any amino acids consumed in excess of an animal's needs are not stored for future use but are disposed of quickly" (Perry, 1966; p. 20).

The use of controlled environments will, in the future, permit research on the influence of light on puberty attainment and

Figure 14 - Proposed model describing attainment of puberty.

Hypothesis: deer can only breed within the shaded area (limited by W, P and L) of the space.

Figure 13 presents a cross-section of part of this model.



P: Critical amount of protein during pre-rutting and rutting period (in excess of protein which is necessary for growth).

W: Critical body weight

L: Critical daylength

For W and perhaps also for P and L exists a range of individual variations.

estrus in female deer and hopefully provide answers to some of the remaining questions, e.g. is puberty elicited as soon as a certain critical short day length is reached or is the stimulus the cumulative effect of darkness. It will also facilitate research on factors influencing puberty attainment and reproduction in general in other seasonally breeding species. For only if photoperiodic conditions equal those of the breeding season of the species can the effect of other factors become clear.

There is no doubt that female black-tailed deer achieve weights during the second summer of their lives that far exceed the critical weight necessary for puberty attainment. The summer browse also provides them with sufficient protein above the maintenance requirements so that the critical protein level is reached. Yet they have to wait for the days to shorten to a certain length before the other essential factors can assert their influence.

Meticulous husbandry was necessary to raise the weight of the captive fawns used in this study above the critical level at a time within the proper day length limits, and commercially produced feed was needed to provide nutrition with protein above the critical level at that time of year. Under these conditions a large percentage of captive female fawns attained puberty regularly, the weights of the precocious and the non-precocious fawns were significantly different. In addition, fawns on a low protein diet which approximated the seasonal decline in natural deer forage failed to attain puberty. These results in combination with the results of other workers led to a hypothetical model describing the influence of body weight, protein and photo-period on puberty attainment.

Appendix A

Fawn retrieval in black-tailed deer (*Odocoileus hemionus columbianus*)

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The mechanism of fawn retrieval by the maternal doe, involving either a dropped (stress situation) or bedded (non-stress situation) fawn is one of several types of survival-specific behaviour patterns which have been considered in ungulate behaviour. White, et al. (White, M., F. Knowlton, and W. Glazener; J. Wildl. Manage., 36(3); 897-905, 1972) described this behaviour in the white-tailed deer, Odocoileus hemionus virginianus, as a direct approach by the doe to within approximately two hundred meters of the fawn, followed by a random search and feed pattern. They noted the neck-out, ears-up attitude of the approaching doe, and attributed this to the alertness of the doe. They also noted the occasional use of a soft "mewing" sound emitted by the doe in order to elicit a response from the concealed fawn. Downing and McGinnes (J. Wildl. Manage., 33(3): 711-714, 1969) noted the high-bounding drop signal employed by the doe in order to conceal her fawn. Linsdale and Tomich (A Herd of Mule Deer, 567pp., 1953), in observations on the Mule deer, O. h. hemionus, noted the neck-out, ears-up attitude of an approaching mother, and briefly mentioned the possibility that a fawn might recognize its mother by individual-specific body attitudes.

Observations were made on the Columbian black-tailed deer, O. h. columbianus, at the University of British Columbia Research Forest, near Haney, B. C., and at Kelsey Bay, on northern Vancouver Island, B. C. A previously undescribed retrieval or "pick-up" behaviour was observed on five occasions. Sound monitoring equipment placed at the fawn drop site indicated that no sound within the range of 200 to 16,000 Hz. was used by the doe or fawn in reunion during these observations, either in fawn location or in the actual pick-up.

The doe approached the fawn in two different ways, depending on whether she was picking up a dropped or a bedded fawn. When retrieving a dropped fawn, the doe approached from downwind, in a zig-zag search pattern (Illustration 1). She then circled the fawn, giving no visible indication of its whereabouts. Foot stomping and snorting were exhibited and appeared to be possible predator-provoking actions. In three observed instances, the fawn was again circled by the doe, who occasionally stopped circling to feed. The doe then approached the fawn's location directly, with her neck outstretched and her ears up and forward, and maintained this position for approximately two to ten seconds while standing over the fawn. This body attitude was very similar to the aggressive stance reported by Cowan and Geist (J. Mammal., 42: 522-526, 1961), and might have constituted a final challenge to any possible intruders in the area. The doe then lowered her head, maintaining the neck-out, ears-up attitude, and stared directly at the fawn for one to five seconds. The fawn then responded by rising and following the mother.

In the instances of retrieval concerning a bedded fawn, the doe did not exhibit the aggressive, defensive behaviour described above. Pick-up was simplified, and involved a direct approach to the fawn's location (Illustration 2). In one smooth movement, the doe outstretched her neck, raised her ears, and looked down intently at her fawn. The fawn responded by rising and following her mother, or suckling her for a few moments.

It was concluded from these observations that this "pointing" attitude (ears up, neck outstretched) in the black-tailed deer is not simply an expression of alertness of the returning doe, but rather an innate signal for the fawn to rise. This pattern of behaviour allows the doe to determine the time of the fawn's retrieval, preventing the fawn from rising at an inopportune time, possibly revealing its location to a nearby predator. A visually oriented signal such as this would also facilitate family-specific reunion of doe and fawn by enabling the doe to scrutinize a fawn prior to actual pick-up.

LEGENDS TO FIGURES

Figure 1 - Doe behaviour during retrieval and pick-up of a dropped fawn:

1) approaching vicinity of fawn;
2) snorting and stamping; aggressive behaviour;
3) circling fawn; no indication of fawn's position;
4) neck out, ears up attitude;
5) "pointing" and staring attitude; fawn rises.

Figure 2 - Doe behaviour during retrieval and pick-up of a bedded fawn:

1) direct and relaxed approach towards fawn;
2) stopping in front of fawn, ears up, fawn may start to respond;
3) "pointing" and staring attitude, less rigid than in Figure 1; fawn rises.

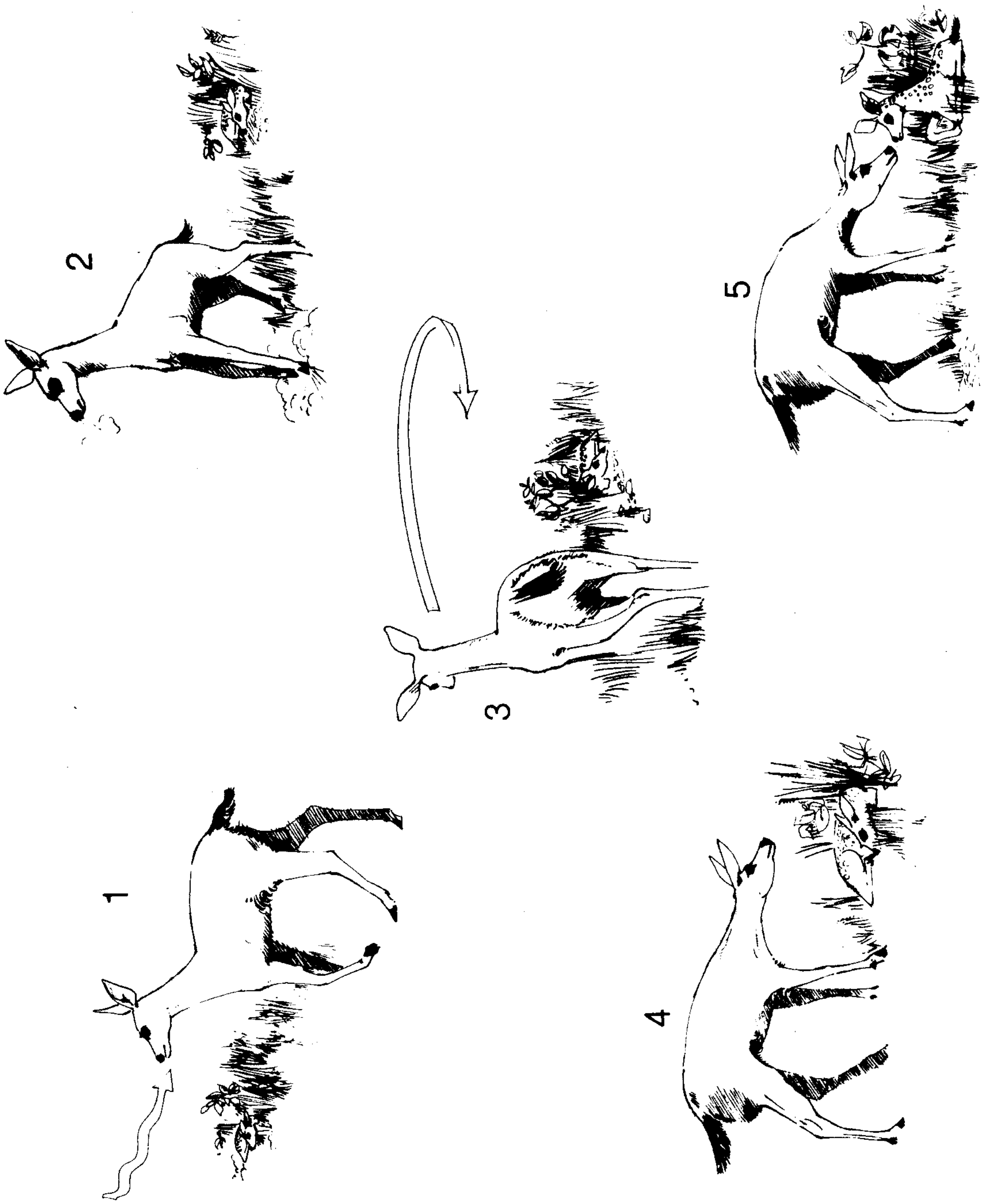

Figure 1

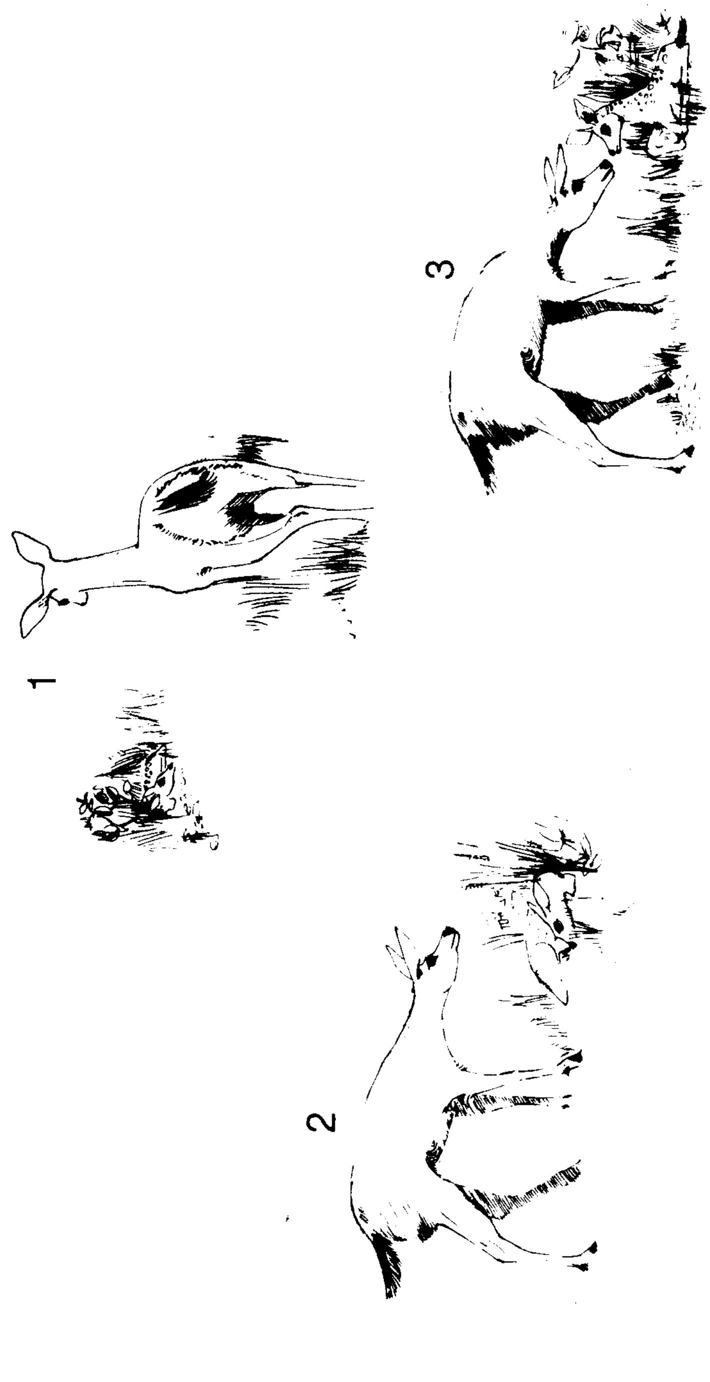

Figure 2

Appendix B

Attainment of early puberty in female black-tailed deer (*Odocoileus hemionus columbianus*)

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ABSTRACT

Female black-tailed deer fawns were hand-raised until four months of age and bred to bucks in their first fall. Over 50% conceived and subsequently gave birth to single fawns. Conceptions occurred later than for wild adults but at weights which equalled the weights of the heaviest wild fawns. A high proportion of the fawns born to fawn does died due to presumed lactation failure. Further work is continuing on the factors governing puberty attainment in this species.

INTRODUCTION

There is plentiful evidence that nutritional status can affect reproductive success and the age at which deer first breed (1, 2, 3, 4). Ovulation rates, birth rates and the proportion of yearlings which breed are all known to be related to range conditions. There has been indirect evidence of conceptions in fawns in the wild. Robinette *et al*. (2) found corpora lutea scars in 7 of 167 yearling mule deer (*O*. *h*. *hemionus*) which indicated conceptions as fawns but none had given birth. In addition no pregnancies were found in 107 fawn tracts. Brown (3) reports three cases of fawn black-tailed deer giving birth in captivity and mentions another instance of a possible conception in a wild fawn where pregnancy was not completed. Thomas and Smith (5) reported a single instance of a wild doe from Vancouver Island with a corpus albicans in November whose age was determined from teeth to be 1 1/2 years old. In a detailed study of breeding on Vancouver Island, Thomas reported no corpora albicantia in the ovaries in 116 yearling females and no corpora lutea in 59 fawns (6). In the deer unit at the University of British Columbia two captive fawns were noted as having ovulated. One was unmated, the other produced a live offspring (5, 7).

On the basis of the above information a project was commenced in 1973 to investigate further the role of nutrition in puberty attainment in this species. The hypothesis was set up that black-tailed fawn does do not achieve sufficient weight in the wild by the time of breeding in November. Further, that under most range conditions a sufficient weight to breed is reached when they are 18 months old. Therefore if growth rates could be maximised under captive rearing conditions, fawns could achieve sufficient weights to breed in their first fall.

METHODS

During June, 1973 23 ♀♀ fawns were captured within ten days of birth. 20 of these were taken from Vancouver Island, mostly from near Kelsey Bay. They were hand-raised for four months and weaned October 1st. This was a much longer period of bottle feeding than used by Bandy (9) whose animals were weaned at an average age of two months. The condensed cows milk used was lower in fat and protein concentration than the milk of the doe (8). However the lactose concentration was considerably higher. From 1st October 20 of these fawns were kept in single pens. From 28th October a 1 1/2 year old buck (whose semen had motile sperm) was introduced to each fawn doe for periods of up to twenty minutes per day depending on the state of sexual interest. After December 18th the fawns were released into a 2 1/2 acre compound which was already occupied by several other bucks and a few females.

RESULTS

While in the individual pens, 6 of the 20 fawn does exhibited estrus between October 28 and December 18. Individuals showed estrus between 1 and 5 times during this period. Estrus was not seen on consecutive days and there was no regular cyclic pattern of repeat of estrus. During estrus the fawn does stood to the buck who was observed to ejaculate. Subsequent observations showed one birth which could have resulted from a conception under this mating regime.

Of the 20 fawn does kept in individual pens and then released into the compound, 10 individuals conceived. One pregnant fawn doe was lost due to accident so that 9 parturitions subsequently occurred. All litters were of single fawns.

Conceptions occurred at weights ranging from 25.5 to 33.5 Kg. (Figure 1). In order to compare these weights with those of wild fawns, we utilized data on 314 dressed fawn weights collected in November of various years during the N.W. Bay study and kindly provided to us by the Nanaimo office of the B. C. Fish and Wildlife Branch. These were converted to total body weights by use of a regression formula (r^2=.987) calculated by Allen Anderson (Wildlife Research Centre, Fort Collins, Colorado) for 56 mule deer (*O. h. hemionus*) under 17 months of age. This formula is $y = 0.0602 + 1.3714x$ (where y = bled weight in Kg and x = eviscerated weight, in kg). The weights of the wild fawns are compared with those of the experimental fawns in figure 1. Many wild fawns which do not breed have achieved weights which exceed the minimum weight at conception of experimental fawns. This result excludes the possibility of a simple threshold effect. We therefore consider our original hypothesis disproved.

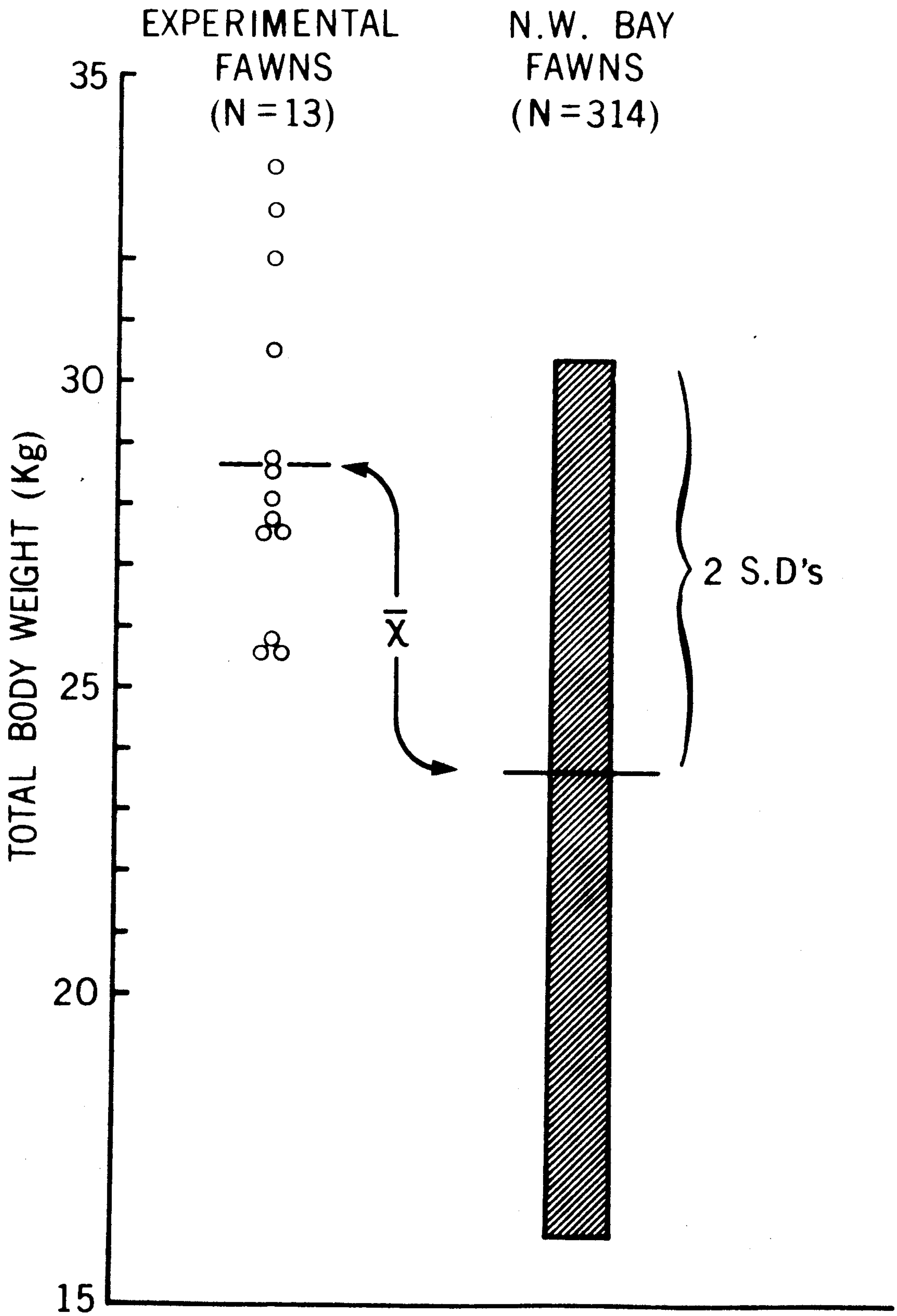
The average date of conception in experimental fawn does kept in pens in November and released into the compound in mid-December was considerably later (Table 1) than the usual breeding period in the wild (November to mid-December; 3, 6).

TABLE I: Birth and conception dates of penned animals.

	Birth Date	Estimated date of Conception*
First birth	June 24	December 2
Last birth	August 8	January 19
Average (N=10)	July 24	January 2

*203 days (3)

In addition to the above animals, three experimental fawn does were released into the compound and ran with several bucks from October 1st onwards. 2 of these conceived at the end of November and the other in early January. It is thus possible that the delayed breeding season in the 10 penned and released fawns may have been due to the experimental conditions. This possibility is being investigated during the 1974 season. However, it is interesting to note that in white-tailed deer (O. virginianus) where fawns breed fairly frequently, these fawns conceive about two weeks later than adults (10).


EXPERIMENTAL FAWNS (N = 13)
N.W. BAY FAWNS (N = 314)
TOTAL BODY WEIGHT (Kg)
35
30
25
20
15
X̄
2 S.D's

Although there was a relatively high conception and birth rate resulting from the breeding of fawn does, the survival of their fawns was poor. Twelve fawns were born (13 conceptions, 1 pregnant female accidentally lost) but 7 of these died between one and four and a half months of age. Post mortems showed these fawns to be emaciated, with stomachs full of the pelleted ration but with no milk. In addition, weekly weighings showed that the weight of these fawns did not increase, and in most cases, decreased, prior to death. These observations suggest strongly that the fawns died due to lactation failure of the mother. It is unlikely that lactation failure was caused by inadequate nutrition as the fawn mothers were on an ad lib. diet of alfalfa and calf starter pellets (20% protein). An older doe on the same diet successfully raised twin fawns. Although the fawn mothers commenced lactation somewhat later than older does, their lactation ceased at a time when older does were still lactating.

ACKNOWLEDGEMENTS

We wish to thank Mrs. E. Gadsby for conscientious animal maintenance and Mr. J. Walters and the staff of the UBC Research Forest, Maple Ridge for ongoing cooperation. A. Anderson (Wildlife Research Centre, Fort Collins, Colorado) kindly calculated the regression formula. This research was financed by grants from the NRC of Canada and the B. C. Fish and Wildlife Branch.

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Appendix C

Changes in the nutrient composition of milk of black-tailed deer during lactation

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There are many reports of the nutrient composition of mammalian milks (reviewed by Ben-Shaul, 1962; Blaxter, 1961). In the majority of cases, with the exception of the work of Arman *et al.* (1974) on red deer (*Cervus elaphus*) such reports describe the composition of single samples at an undesignated stage of lactation. The nutrient contents of small numbers of irregular samples of milk from deer of the genus *Odocoileus* have been reported (*O. virginianus*: Murphy, 1960; Silver, 1961; Youatt *et al.*, 1965; Jenness, 1974. *O. hemionus*: Hagen, 1951; Browman and Sears, 1955; Kitts *et al.*, 1956; Jenness, 1974). As part of ongoing studies on female puberty and reproduction of Columbian black-tailed deer (*O. h. columbianus*) we report here changes in milk composition throughout the lactation period.

Three semi-tame does were removed from a holding paddock in April 1975 and kept in individual 2.75 x 3.65 m pens. Alfalfa hay and 20% protein calf starter pellets were provided *ad lib.* with frequent supplements of fresh salmonberry (*Rubus spectabilis*) and willow (*Salix sp.*). Doe 0 was three or more years of age and gave birth to twin fawns on May 19. Doe 10 was 2 years old and gave birth to a single fawn on June 5. Doe 1 was 1 year old and gave birth to twin fawns on June 9, one of which was removed for hand rearing on June 10. Milk samples were taken each Monday, Thursday and Sunday prior to June 29. Samples taken within 7 day periods after lactation commenced were combined and analyzed as one sample. After June 30 samples were taken each Monday and Thursday. With two exceptions, these samples were combined into two-week bulk samples for the separate individuals and so analyzed.

Fawns were separated from does the evening prior to the day of sampling. Does were immobilized with succinylcholine (Anectine, Burroughs Wellcome) injected intramuscularly into the hindquarters. Dosages ranged from 0.06 to 0.115 milligrams/ kilogram body weight, the minimum dose being most commonly used. The normal effect was relaxation of the muscles of the extremities and neck only, but occasionally respiratory arrest occurred. Artificial respiration was then administered and in all instances the does recovered with no further complications. Once immobilised, 40 international units of oxytocin (Rogar/S.T.B., division of BTI Products Inc.) were injected into the jugular vein to induce milk let-down. Milking was done by hand.

The udder of this species consists of four separate quarters each with a single teat canal. The posterior quarters are much larger than the anterior and produce by far the larger proportion of total milk output. Until the 22nd to 25th week of lactation, depending on the flow from each doe, one posterior quarter and one anterior quarter were emptied at each sampling. Petersen (1950) noted that the composition of cows milk can change during a single milking due to the presence of an agglutinin which causes clustering of the fat globules. Although it is not known if this phenomenon occurs in deer, as a precaution the total yield from the two quarters was thoroughly mixed and a 20 cubic centimeter sample taken for analysis. After the 22nd to 25th week of lactation insufficient milk was obtained by the above method, so all four quarters were emptied, the milk mixed and 20 cc preserved. Towards the final stages of lactation it sometimes became necessary to analyze less than 20 cc. Milk samples were preserved with potassium dichromate and kept at 4°C until analyzed.

The protein content was determined by the dye binding method (Ashworth et al., 1960) using standard curves from cow's milk. The lactose content was analyzed by the method of Trevlyn and Harrison (1952), using α-lactose monohydrate as a standard, and fat content was determined with the Mojonnier milk tester (Mojonnier, 1925).

The changes in nutrient composition of the milk are shown in Fig. 1. The lactose content increased slightly over the first month of lactation and then steadily declined. An analysis of variance for each doe showed a significant change ($P<0.05$) for does 0 and 10 but not for the yearling doe 1. In the red deer, Arman et al. (1974) reported mean lactose concentrations of between 4.1 and 4.7 g/100 milliliters which are similar to the values reported here for the first two months of lactation. The red deer, however, showed no decline in lactose levels as lactation progressed.

Total protein content increased steadily in the milk of all does until the sixth month of lactation. An analysis of variance showed significant changes ($P<0.05$) in each doe until this time. The protein content then declined at slightly different times in each doe. During the increase period total proteins ranged from 6.5% to just over 11%, values similar to those for the red deer (Arman et al., 1974). However, there is no clear indication in the red deer data of a decline in protein content at the end of lactation.

For each female the percentage of fat increased suddenly early in lactation, then declined, and then steadily increased until the sixth month. Analyses of variance for each doe showed significance ($P<0.05$) until this period. The fat content of the milk of the two younger does (1 and 10) then suddenly declined. The fat content of the milk of the older doe (0) dropped also in weeks 26 and 27 but then recovered and stayed relatively high until the end of sampling in mid-January. The fat content of red deer milk showed a similar pattern of increase but the absolute values were lower (Arman et al., 1974). The percentage of fat (10-20%) reported here is considerably higher than that reported previously for spot samples of blacktailed deer milk (Hagen, 1951: 8.3%; Kitts et al., 1956: 10.2-10.5%). The absolute values and pattern of change are most like those of the Dall sheep (Ovis dalli dalli) as reported by Cook et al. (1970). Ben-Shaul (1962) suggested that the fat content of milk is related to the interval between sucklings in comparisons between species. In species whose milk has a high fat content, sufficient energy is transmitted at each feeding to allow a long interval to the subsequent feeding. This relationship would seem also to hold in black-tailed deer as the fat content of milk increases during lactation (fig. 1). In a separate study of suckling behaviour, we have noted that the interval between sucklings increases as lactation proceeds.

The end of lactation in the two younger does was preceded by sudden drops in fat and protein content. This coincided roughly with the timing of reduced milk yield as indicated by the amount obtained by hand milking. The older doe (0) also apparently reduced her yield at this time but did not dry up and maintained an ongoing smaller yield. Future work is intended to document changes in milk yields in this species.

We have shown (Mueller and Sadleir, 1975) that a high proportion of fawns of this species will breed under captive conditions although such breeding does not occur in wild populations. It is of interest that doe 1, which conceived at 6 months of age and gave birth at 12 months, was able to produce milk of quality equivalent to two older does throughout a complete lactation. The three differently-aged does each produced milk with similar patterns of nutrient composition.

During this study the solid food intake of fawns was not recorded. One of us (C.C.M.) has frequently seen fawns eating solid food at one week of age and ruminating at 36 to 73 ($\bar{x}$ = 50) days of age. Ongoing work will attempt to describe the increase in solid food intake of fawns.

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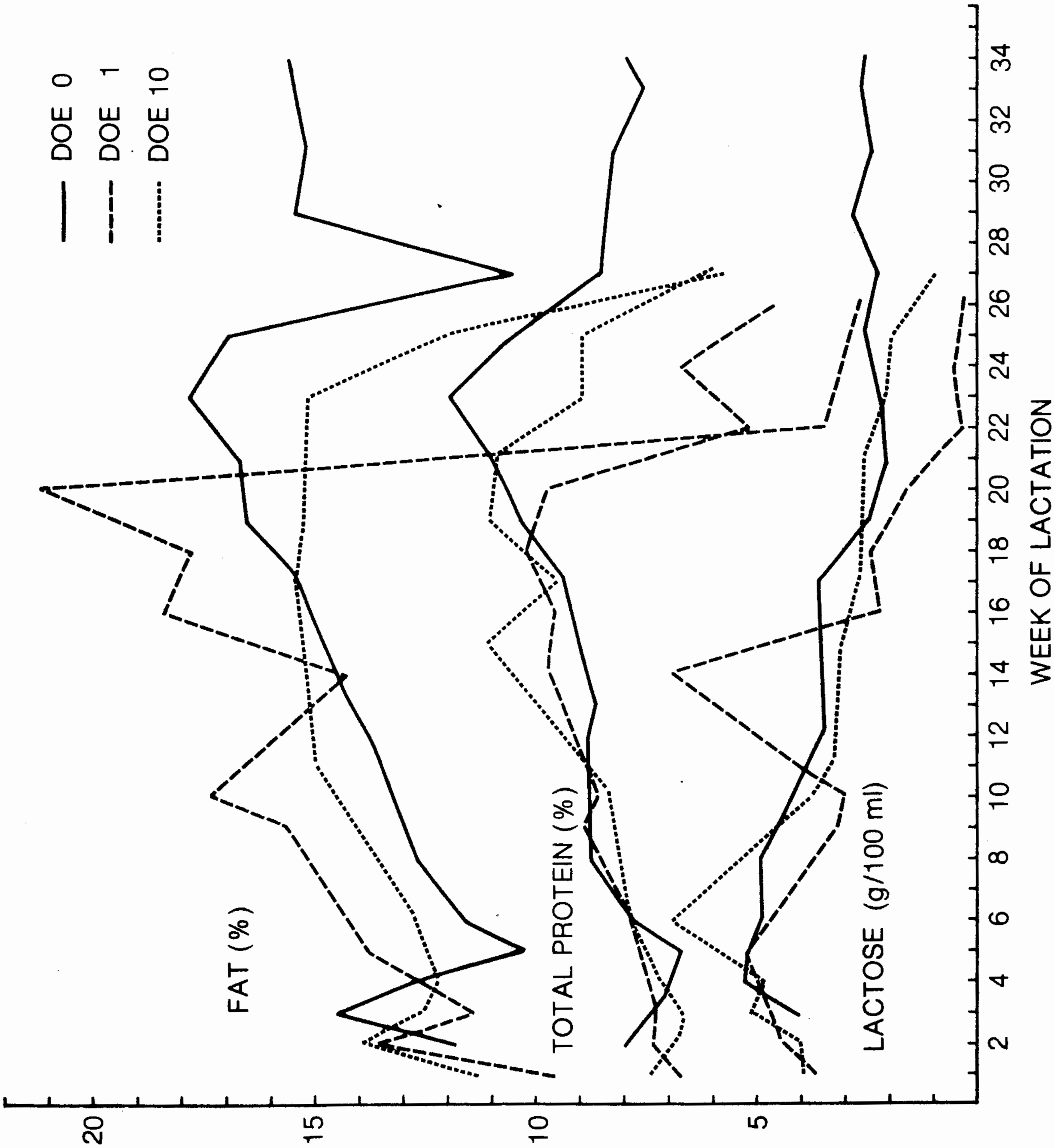
Figure 1 - Changes in nutrient composition of the milk of three nursing black-tailed deer. Doe 1 and Doe 10 ceased lactation on weeks 26 and 27 respectively. Doe 0 continued lactation after sampling ceased.



DOE 0
DOE 1
DOE 10
FAT (%)
TOTAL PROTEIN (%)
LACTOSE (g/100 ml)
WEEK OF LACTATION
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
5
10
15
20

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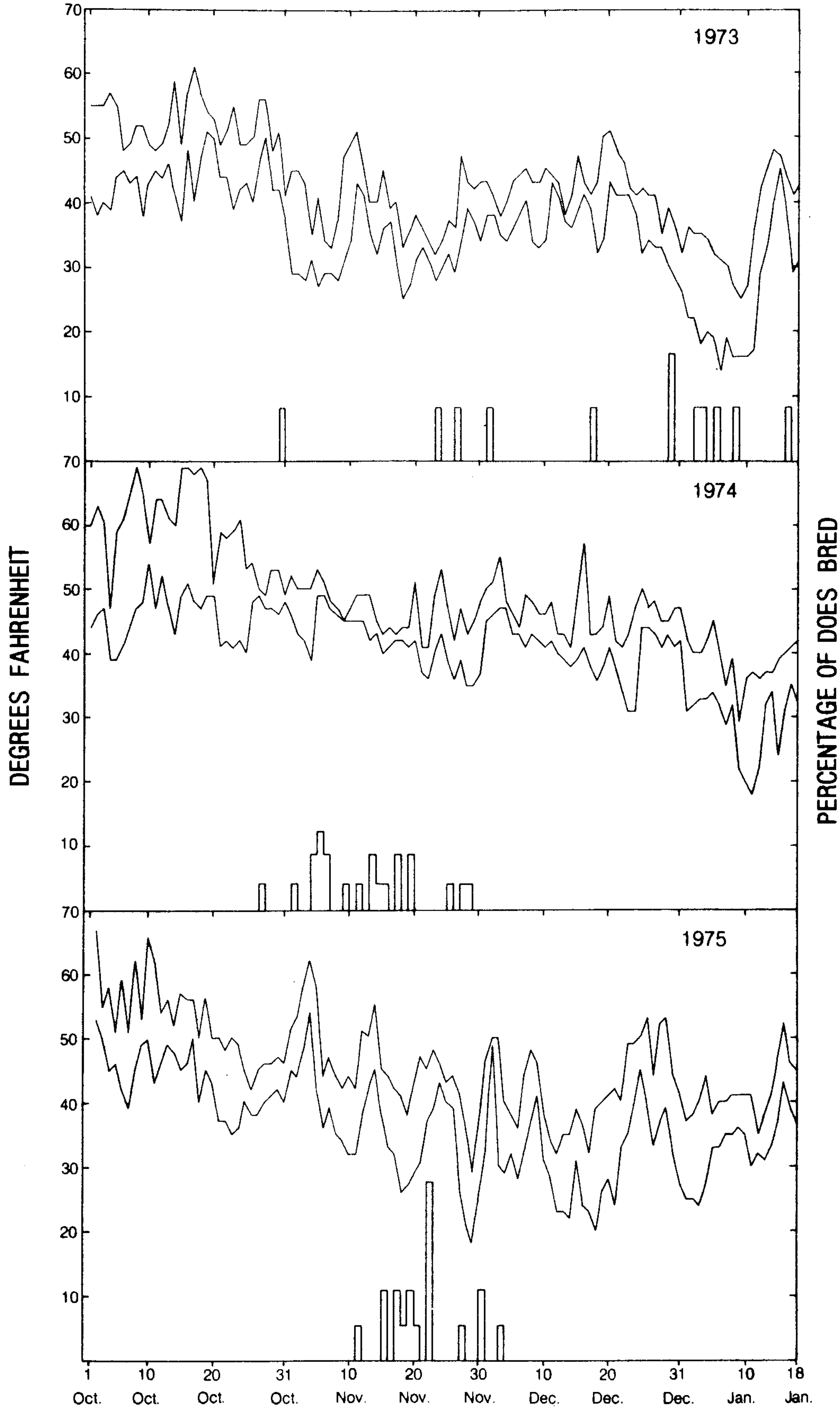
Appendix D

Relation between local temperature (daily maxima and minima) and breeding in female black-tailed deer.

Location: U. B. C. Research Forest, Maple Ridge, British Columbia.

According to Linsdale and Tomich (1953) cold tends to increase rutting activity, and extremely warm days may reduce activity so as to make the rut scarcely discernible. However, extremely cold weather may retard breeding activity (Brown, 1961).



Histograms indicate % of does bred.

Appendix E

Fawn birth data — only Kelsey Bay stock

Fawn birth data - only Kelsey Bay stock

Tag #	Sex	Birth Date	Weight	Heart girth	Hindfoot length	Age of Dam (years)	# of Parturition	Weight of Dam
				A. Twin fawns				
17-B	f	19-6-75	1.65	25.4	20.0	2	2	45.5
23-C	f	17-6-75	1.9	26.0	20.3	2	2	38.4
24-B	f	9-6-75	2.0	25.7	21.3	2	1	40.9
K-A	f	2-6-76	2.0			2	1	49.1
K-B	f	2-6-76	2.1			2	1	49.1
I-B	f	9-6-75	2.15	29.5	21.8	1	1	38.1
17-C	f	19-6-75	2.2	29.2	21.6	2	2	45.5
22-C	f	28-5-75	2.2	28.2	20.6	2	2	41.8
22-D	f	5-6-76	2.2			3	3	45.9
23-E	f	13-6-76	2.2			3	3	43.6
14-C	f	25-5-75	2.25	25.8	21.9	2	2	38.2
E-C	f	13-6-76	2.35			2	2	37.7
F-B	f	13-6-76	2.35			2	1	44.5
24-D	f	10-6-76	2.35			3	2	45.5
24-C	f	10-6-76	2.5			3	2	45.5
16-B	f	11-6-75	2.5	28.3	23.2	2	2	39.0
16-C	f	11-6-75	2.5	28.0	23.2	2	2	39.0
F-A	f	13-6-76	2.6			2	1	44.5
2-B	f	28-5-75	2.65	29.5	23.5	2	2	45.0
2-C	f	28-5-75	2.65	27.9	23.8	2	2	45.0
3-C	f	20-6-75	2.7	30.2	23.2	2	2	39.1
22-E	f	5-6-76	2.7			3	3	45.9
2-E	f	6-6-76	2.8			3	3	50.0
16-E	f	9-6-76	2.95			3	3	41.8
5-C	f	3-6-75	3.0	30.5	23.5	2	2	40.5
2-D	f	6-6-76	3.0			3	3	50.0
15-E	f	13-6-76	3.05			3	3	51.8
23-D	m	13-6-76	2.0			3	3	43.6
18-B	m	10-6-76	2.2			3	2	54.5
I-A	m	9-6-75	2.2	27.6	22.2	1	1	38.2
14-B	m	25-5-75	2.4	29.5		2	2	38.2
22-B	m	28-5-75	2.4			2	2	41.8
21-A-B	m	8-6-76	2.35	29.2	22.9	2	1	43.2
23-B	m	17-6-75	2.45	29.5	21.3	2	2	38.4
24-A	m	9-6-75	2.45	27.3	21.9	2	1	40.9
E-B	m	9-6-75	2.5			2	2	37.7
18-C	m	10-6-76	2.5			3	2	54.5
15-C	m	29-5-75	2.55	28.3	22.0	2	2	45.0
3-B	m	20-6-75	2.6	30.2	23.2	2	2	39.1
8-B	m	27-5-75	2.6	29.2	22.9	2	2	40.5
21-A-A	m	8-6-76	2.6			2	1	43.2
11-E	m	18-6-76	2.65			3	3	
8-C	m	27-5-75	2.8	30.5	23.8	2	2	40.5
11-B	m	6-6-75	2.95			2	2	48.0
15-B	m	29-5-75	3.0	30.5	22.9	2	2	45.0
15-D	m	13-6-76	3.05			3	3	51.8
11-C	m	6-6-75	3.1			2	2	48.0
16-D	m	9-6-76	3.15			3	3	41.8
5-B	m	3-6-75	3.15	31.1	23.8	2	2	40.5
11-D	m	18-6-76	3.2			3	3	
				B. Single fawns				
J-A	f	21-6-75	2.55			2	1	42.7
3-A	f	2-8-74	2.55			1	1	36.4 •
19-A	f	12-6-75	2.55	29.5	22.2	2	1	42.5
18-A	f	7-6-75	2.65	28.6	22.9	2	1	48.2
16-A	f	26-6-74	2.7			1	1	36.6 *
5-A	f	8-8-74	2.75			1	1	31.8 **
17-A	f	31-7-74	2.8			1	1	37.3 *
21-A	f	21-7-74	2.85			1	1	37.3 *
2-A	f	21-7-74	3.1			1	1	40.0 *
10-A	m	5-6-75	2.30	28.6	22.9	2	1	45.5
E-A	m	24-5-75	3.15	30.5	23.5	1	1	30.9
11-A	m	25-7-74	3.30			1	1	46.8 *
14-A	m	23-6-74	3.30			1	1	38.6 *
15-A	m	9-6-74	3.40			1	1	39.5 *
16-C-A	m	8-7-76	3.50			1	1	34.5 ***

Weight in kilograms, measurements in centimeters,
All measurements, unless indicated otherwise,
within 24 hours of birth.

- • Sept. 11
- ** April 5
- *** July 14

Appendix F

Life histories and breeding records of experimental does, 1973 - 1976.

KEY:
□ -hand-raised; H-ad libitum feedration; L-70% feedration; HP-high (20%) protein feed; LP-low (15%-10%-7%-10%) protein feed; + -died

SPRING 1973				FALL 1973	SPRING 1974				FALL 1974	SPRING 1975				FALL 1975	SPRING 1976				
Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt in Kg.)		Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt. in Kg)		Tag No.	Sex	Birth Date	Birth Weight		Tag No	Sex	Birth Date	Birth Weight	
[1] L	♀	(8-6)	(2.6)	+3-2-74, preg.															
[2] H	♀	(10-6)	(4.0)		2-A	♀	21-7	3.1	+21-8-74	2-B	♀	28-5	2.7	+11-9-75	2-D	♀	6-6	3.0	
										[2-C]	♀	28-5	2.7	+9-1-76	2-E	♀	6-6	2.8	
[3] H	♀	(10-6)	(3.3)		3-A	♀	1-8	2.6	+5-9-74	3-B	♂	20-6	2.6		3-D				+24-2-77
										[3-C] LP	♀	20-6	2.7		3-E				released 20-8-76
[5] H	♀				5-A	♀	8-8	2.8	+23-1-75	5-B	♂	3-6	3.2		5-D				
										5-C LP	♀	3-6	3.0		5-E				released 20-8-76
[8] H	♀	(14-6)	(2.7)		8-A	♂	15-6		+7-10-74	8-B	♂	27-5	2.6		8-D	♂			shipped 30-9-76; shipped 30-9-76
										8-C	♂	27-5	2.8		8-E	♂			shipped 30-9-76
[10] H	♀	(15-6)	(3.7)							10-A	♂	5-6	2.3						shipped 18-6-76; shipped 30-9-76
[11] H	♀	(15-6)	(4.4)		11-A	♂	25-7	3.3		11-B	♂	6-6	3.0	+5-11-75; released 15-8-75	11-D	♂	18-6	3.2	shipped 30-9-76; shipped 30-9-76
										11-C	♂	6-6	3.1	+20-9-75	11-E	♂	18-6	2.7	shipped 30-9-76

SPRING 1973				FALL 1973	SPRING 1974				FALL 1974	SPRING 1975				FALL 1975	SPRING 1976				
Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt. in Kg.)		Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt. in Kg)		Tag No.	Sex	Birth Date	Birth Weight		Tag No.	Sex	Birth Date	Birth Weight	
12 L	♀	(15-6)	(3.3)	+20-11-73															
14 H	♀	(15-6)	(3.2)		14-A	♂	23-6	3.3	+9-11-74	14-B	♂	27-5	2.4		14-D				
										14-C	♀	27-5	2.3	+26-6-75	14-E				
15 H	♀	(16-6)	(4.3)		15-A	♂	9-7	3.4	+20-10-74	15-B	♂	29-5	3.0		15-D	♂	13-6	3.1	shipped 18-6-76
										15-C	♂	29-5	2.6	+30-7-75	15-E	♀	13-6	3.1	+1-12-76
16 L	♀	(16-6)	(2.6)		16-A	♀	26-7	2.7	+6-10-74	16-B HP	♀	11-6	2.5		16-D	♂	9-6	3.2	+5-7-76 released 20-8-76
										16-C HP	♀	11-6	2.5		16-E	♀	9-6	3.0	shipped 23-3-77
															16-C-A	♂	8-7	3.5	
17 L	♀	(16-6)	(2.5)		17-A	♀	31-7	2.8	+4-9-74	17-B HP	♀	19-6	1.7		17-D	♀	13-6	2.5	+12-7-76 released 20-8-76 shipped 30-9-76
										17-C HP	♀	19-6	2.2	+10-1-76	17-E	♀	13-6	2.5	stillborn
18 H	♀	(17-6)	(4.4)							18-A HP	♀	7-6	2.7	+16-10-75	18-B	♂	10-6	2.2	
															18-C	♂	10-6	2.5	
19 L	♀	(20-6)	(2.8)							19-A	♀	11-6	2.6						released 20-8-76
21 L	♀	(18-6)	(3.4)		21-A	♀	21-7	2.9	+1-11-74						21-A-A	♂	8-6	2.6	shipped 23-3-77
															21-A-B	♂	8-6	2.4	

SPRING 1973				FALL 1973	SPRING 1974				FALL 1974	SPRING 1975				FALL 1975	SPRING 1976				
Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt in Kg.)		Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt. in Kg)		Tag No.	Sex	Birth Date	Birth Weight		Tag No	Sex	Birth Date	Birth Weight	
22 H (boxed)	♀	(19-6)	(4.5)		22-A	♀	18-6			22-B	♂	28-5	2.4		22-D	♀	5-6	2.2	+25-6-75
										22-C HP	♀	28-5	2.2		22-E	♀	5-6	2.7	released 20-8-76 +24-6-76
23 L (boxed)	♀	(19-6)	(3.7)		23-A	♂	28-7			23-B	♂	17-6	2.5	released 15-8-75	23-D	♂	13-6	2.0	shipped 18-6-76 shipped 30-9-76
										23-C (boxed) LP	♀	17-6	1.9		23-E	♀	13-6	2.2	released 20-8-76
24 H (boxed)	♀	(20-6)	(4.6)							24-A	♂	19-6	2.5	+24-8-75	24-C	♀	10-6	2.5	shipped 23-3-77
										24-B	♀	19-6	2.0	+4-9-75	24-D	♀	10-6	2.4	
28 L	♀									28-A	♂	29-5	1.8	+1-6-75	28-C	♀	11-6	2.7	+16-6-76 shipped 4-76
										28-B	♀	29-5	1.7	+7-6-75	28-D	♀	11-6	2.7	+21-6-76
27 L	♀									27-A aborted	♂	11-6	0.9		27-C	♂	24-6	2.3	+12-6-76 shipped 4-76
										27-B	♂	11-6	0.8		27-D	♂	24-6	3.0	
29 (boxed) Washington H	♀									29-A	♂	5-6	3.0	released 1-76	29-C				
										29-B	♂	5-6	2.7	+16-9-75	29-D				

SPRING 1973				FALL 1973	SPRING 1974				FALL 1974	SPRING 1975				FALL 1975	SPRING 1976				
Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt. in Kg.)		Tag No.	Sex	Birth Date (Capture Date)	Birth Weight (Capture Wt. in Kg)		Tag No.	Sex	Birth Date	Birth Weight		Tag No.	Sex	Birth Date	Birth Weight	
30 Washington H	♀									30-A	♂	1-6	2.8	+7-6-75	30-C	♂	8-6	3.2	+12-6-76
										30-B	♂	1-6	2.6	+2-6-75	30-D	♀	8-6	3.1	
31 Washington H	♀									31-A LP	♀				31-B	♀	5		released 20-8-76
															31-C	♀	5		
O adult age unknown H	♀				O-A	♂	22-5	3.1		O-C	♂	19-5	3.4	not mated	O-B-B	♂	21-6	3.1	shipped 4-76; shipped 4-76
					O-B	♀	22-5	2.7		O-D	♀	19-5	3.4						
										O-B-A	♂	21-8	3.0	+6-9-75	O-B-C	♀	21-6	3.1	shipped 23-3-77
					E	♀	(13-6)	(2.1)		E-A	♂	24-5	3.2		E-B	♂	13-6	2.5	
															E-C	♀	13-6	2.4	
					F	♀	(14-6)	(3.7)							F-A	♀	13-6	2.6	+1-12-76
															F-B	♂	13-6	2.4	released 8-3-77
					I	♀	(15-6)	(4.2)		I-A	♂	9-6	2.2	not mated					
										I-B LP	♀	9-6	2.2						shipped 30-9-76
					J	♀	(15-6)	(2.6)							J-A	♀	21-6	2.6	shipped 30-9-76; shipped 30-9-76
					K	♀	(21-6)	(4.0)							K-A	♀	2-6	2.0	+18-6-76
															K-B	♀	2-6	2.1	shipped 30-9-76; shipped 30-9-76

Appendix G

Protein levels of major browse species in summer and winter on Vancouver Island, British Columbia. Rochelle, J. (pers. comm., 1976)

Vancouver Island: Winter Crude Protein Levels of Major Winter Forage Plants in Percent of Oven Dried Weight

Western Hemlock (*Tsuga heterophylla*, Sargent)	5
Western Red Cedar (*Thuja plicata*, Don)	5
Salal (*Gaultheria shallon*, Pursh)	5
Blueberry (*Vaccinium alaskaense*, Howell)	7
Red Huckleberry (*Vaccinium parvifolium*, Smith)	7
Sword Fern (*Polystichum munitum*, Presley)	9
Lichen (*Alectoria* sp.)	2

Vancouver Island: Maximum (approx., cutover and timbered area combined) Levels of Crude Protein in Percent and Month at which they occur (Oven Dried Weight)

Douglas Fir (*Pseudotsuga menziesii*, Franco)	10	June
Western Hemlock (*Tsuga heterophylla*, Sargent)	8	June
Western Red Cedar (*Thuja plicata*, Don)	6	April
Blueberry (*Vaccinium alaskaense*, Howell)	19	May
Red Huckleberry (*Vaccinium parvifolium*, Smith)	20	May
Salal (*Gaultheria shallon*, Pursh)	12-13	June
Sword Fern (*Polystichum munitum*, Presley)	16-20	June
Fireweed (*Epilobium angustifolium*, Linné)	25	May
Bracken Fern (*Pteridium aquilinum*, Kuhn)	35	May

Appendix H

Miscellaneous observations during the course of this study.

1. A suspected case of monozygotic twins

In 1975 a primiparous 2 year old doe of Washington stock gave birth to male twins with identical pathological deformities. (Brachygnathia inferior, deformation of distal parts of all four legs, depigmentation on left abdomen and chest). The total identity of these fawns suggests that they were monozygotic twins. The birth of monozygotic twins in black-tailed deer is a rare occurrence as indicated by the proportions of homo- and hetero-sexual pairs of twins (Table XIV) and the ratio of corpora lutea to number of fawns per doe (close to 1:1, Taber and Dasmann, 1957).

2. Compensatory weight growth

Two fawns whose early growth was severely retarded due to coccidiosis (time to double birth weight: #16-E -- 42 days, #15-E -- 45 days) showed remarkable compensatory weight growth after they had regained their health. From 25 to 175 days (125 days resp.) of age the following weights (in kg) were recorded at 50 day intervals: #16-E -- 4.8, 11.6, 21.3, 27.0; #15-E -- 4.5, 12.6, 25.5. Both animals, therefore, achieved above average weights in spite of their early illness but neither one attained puberty (#16-E: ultrasonic fetal pulse detection after Lindahl, 1971, was negative at 274 days of age; #15-E: killed by buck at 164 days of age, ovaries were infantile). This is in accordance with Cowan and Wood's (1955) statement that "a setback when growth rate is high is likely to lead to animals that depart from the norm of the species" (p. 335) because physiological time is irrecoverable although sidereal time may be regained (McMeekan and Hammond, 1940).

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