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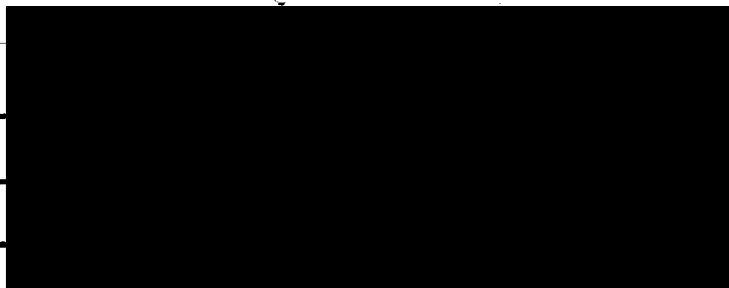
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**LA THÈSE A ÉTÉ
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A QUANTITATIVE ANALYSIS OF THE FEEDING BEHAVIOR OF SUCKLING
BLACK-TAILED DEER (Odocoileus hemionus columbianus)

by

Richard L. Drinnan

B.Sc., Simon Fraser University, 1972.

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences



Richard L. Drinnan 1981

SIMON FRASER UNIVERSITY

April 1981

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ABSTRACT

Though the nourishment of fawns in the first weeks of life may strongly influence the growth and vigor of future deer populations, quantitative studies of nursing and suckling behaviors are lacking. In this study, 5 suckling behaviors of black-tailed deer (Odocoileus hemionus columbianus) fawns were defined and quantified. Seventeen captive, dam-raised fawns were observed continuously over 24 h periods; the frequency, duration and success of suckling were noted; the quantity of milk consumed was estimated; and the weights of fawns were periodically recorded from birth to age 4 months.

During the first 90 days, the frequency and duration of suckling declined, but the efficiency of suckling increased. Milk consumption did not decline until after age 60 days. From birth to 25 days, heavier-born fawns suckled more frequently, consumed more milk and weighed more at 25 days than lighter-born fawns. Differences of suckling behavior were noted between male and female fawns, single and twin fawns, fawns born to dams of different parity, and fawns of different birth weights. Fawns initiate more suckling bouts and suckling attempts than dams, but dams terminate more suckling attempts than fawns.

The validity of some of these observations is dubious because of small sample sizes. Possible effects of captivity on suckling behaviors are discussed.

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I. INTRODUCTION

Although the biology of North American deer of the genus Odocoileus has been intensively studied, relatively little is known of their suckling behavior. Knowledge of suckling behavior can be applied to the assessment of fawn mortality in relation to winter and spring nutritional status of the dam (Verme, 1963; Murphy and Coates, 1966; Langenau and Lerg, 1976) and to breeding programs undertaken in zoological gardens (Cowan, 1974; Kiley, 1974; C.R. Schroeder, personal communication, 1977).

Because ingestion of milk is the final step in the formation of the mother-young bond (Fraser, 1976), suckling behavior is critical to offspring acceptance by the dam during the immediate post partum period (Collias, 1956; Lent, 1974). This ingestive behavior is necessary for post natal growth of the young (Kitts, et al., 1956; Norden et al., 1970; Robbins and Moen, 1975; Sadleir, 1980b) and the subsequent development of social behavior toward other conspecifics (Scott, 1956; Paatz, 1976). Late weaning of fawns may impart severe nutritional stress upon the dam which could affect her future reproductive potential (Sadleir, 1969; Bahnak et al., 1979; Woolfe and Harder, 1979) as the costs of lactation are energetically greater than any other reproductive processes (Moen, 1978).

Further understanding of the behavioral processes of weaning, combined with investigations of milk consumption and nutritional and physiological statuses of both dam and fawn, are necessary to evaluate parental investment and weaning conflicts (Trivers, 1974).

Numerous accounts of parturitional and immediate post natal behavior are available for white-tailed deer, Odocoileus virginianus, (Haugen and Davenport, 1950; Severinghaus and Cheatum, 1956; Haugen and Speake, 1957; Michael, 1964; White et al., 1972; Townsend and Bailey, 1975; Paatz, 1976; Langenau and Lerg, 1976; LaGory, 1980) and some for black-tailed deer, O. hemionus columbianus (Golley, 1957; Miller, 1965) and mule deer, O. h. hemionus (Dixon, 1934; Linsdale and Tomich, 1953; Truett, 1977). With a few exceptions (Linsdale and Tomich, 1953; Townsend and Bailey, 1975; Paatz, 1976; Langenau and Lerg, 1976), these reports provide few, if any, quantitative data on fawn suckling behaviors, mother-young bond formation and the weaning process.

Townsend and Bailey (1975) reported that 3 captive white-tailed deer dams intensively licked their twin fawns and stimulated them to rise and to first suckle within an average of 36 minutes following birth. Although the first-born of twins rose "significantly" sooner (\bar{x} =19.4 min; range=11-34 min; n=3) than the second-born of twins (\bar{x} =29.4 min; range=15-40 min; n=3), the time at which first suckling attempts occurred after

birth were not "significantly" different for either twin (\bar{x} =36 min; range=21-46 min; n=6). These authors suggested that intensive maternal licking of the neonate facilitates rapid mother-young bonding and, that second-born fawns may suckle sooner after arising than their siblings possibly due to a rapid orientation towards the udder facilitated by tail wagging of the first-born fawn while being nursed.

Langenau and Lerg (1976) supported Townsend and Bailey's (1975) claim that suckling is socially facilitated in twin white-tailed deer fawns and suggested that this influences the duration of suckling by twins compared to single fawns. During the first 72 h post partum, twin fawns suckled on average for a duration of 50.7 s/h while single fawns suckled for 19.8 s/h. In 9 instances of fawn mortality within 72 h post partum, all were due to maternal rejection of fawns, exhibited by a lack of licking and grooming of neonates, an unwillingness to nurse fawns and, in one instance, a dam aggressively kicked a fawn when it attempted to suckle. These authors suggested that winter food availability during gestation may be instrumental in the maternal rejection of fawns. Eight of 9 rejected fawns were born to dams maintained on 50% ad libitum diets from January through March compared to does maintained on either ad libitum or 75% ad libitum dietary regimes. Low diet (50% and 75% ad libitum) dams nursed their twin fawns less frequently and for shorter periods than high diet (ad libitum) dams.

Linsdale and Tomich (1953) reported that free ranging mule deer dams nursed their twin fawns (ages unknown) simultaneously at irregular periods during most of the day, except between 0130 and 0530 h. Nursing periods occurred every 4.5 h on average, exhibited peak frequencies at 0600 h, contained from 1 to 6 suckles spaced 5.6 min apart, and lasted up to an hour. During the first few weeks of the fawning season, dams initiated nursing periods and fawns terminated suckles but after this period the pattern was reversed. The average duration of suckling declined from 155.7 s to 20.8 s as the fawns increased in age. The frequency of both nursing periods and sucklings declined until fawns were apparently weaned at 5 months.

Faatz (1976) reported that vocalizations in captive and free ranging white-tailed deer play a major role in the initiation of nursing and suckling. In most cases the dam initiated nursing periods by approaching the bedded fawn and calling to it in a low grunt and, if the fawn did not respond, the dam employed a higher pitched grunt call. Fawns employed two types of calls directed towards the dam. These calls may serve to attract attention to the fawn and to solicit nursing. A low whine call audible from 5 m was given by the fawn either before nursing periods, as it approached the dam to suckle, or during nursing periods, or after suckling while being groomed by the dam. The frequency of the fawn's low whine call was associated with nursing frequency and declined as the fawn aged. A high

whine call was employed by fawns when the low whine call failed to elicit maternal care and, if followed by a reciprocal low grunt call from the dam, usually resulted in suckling by the fawn.

Licking of a fawn's anal-genital region by a dam served as a mechanism of fawn identification prior to nursing (Faatz, 1976). Nursing frequency averaged 6/24 h (N=22) throughout the first 4 months of age. During the first week of age single fawns were nursed 4-5 times/24 h and twins were nursed 3-5 times/24 h. The first suckle in any nursing period was usually the longest and the length of suckling/nursing period was related to the duration of anal licking. Suckling duration declined with age from 2 to 17 weeks and was less than 1 min/suckling after the eighth week. Fawns terminated all sucklings during the first week after which either dam or fawn terminated contact with the teat. Dam terminations of all sucklings occurred after one month of age. Weaning probably began at 3 months and was completed by 4 months (Faatz, 1976).

Other than the studies cited above no quantitative descriptions of suckling behavior from birth to weaning of known aged fawns of the genus Odocoileus are available. Consequently little is known of the relationships between suckling activity, milk consumption and fawn growth. Comparisons between suckling frequency and milk composition of many mammal species are presented by Ben Shaul (1962). Species which nurse frequently

generally produce a milk low in fat while those species whose young are often left secluded for long periods between nursings produce a milk rich in fat. In studies on black-tailed deer, Mueller and Sadleir (1977) reported the changes in milk constituents during lactation. They found that milk fat content increases as lactation progresses and that this increase corresponds to increased intervals between suckling periods as fawns increase in age. Maternally raised black-tailed deer fawns exhibit extremely high growth rates during their early life (Cowan and Wood, 1955). During the first week of life fawns were found to gain 10 percent of their body weight per day while during the following 2 weeks this rate of gain was 5 percent. Reduced neonatal mortality in this species, due to rapid growth during the first 2 weeks of life, has been attributed to the high quality of the milk produced by the dam during this period (Kitts et al., 1956). Any slight stresses imposed upon the fawn by environmental events such as reduced milk production by the dam or energy loss by the fawn at this time may result in major disruptions to normal growth (Cowan and Wood, 1955). Although Mueller and Sadleir (1980) reported that growth in black-tailed deer fawns was difficult to separate into the discrete growth phases suggested by Cowan and Wood (1955) they did find that light birth-weight fawns exhibited compensatory growth by growing at greater daily rates than heavier-born fawns during the first 30 days. These authors suggested that this

differential growth may result from lightweight fawns consuming more milk per unit of body weight than heavy-born fawns.

Subsequent investigations on milk consumption and growth of black-tailed deer fawns by Saddleir (1980b) revealed that milk was the single most important food item contributing to growth in the first 25 days of life. During this period fawn milk consumption was found to correlate significantly and positively with the crude growth rate but was not significantly correlated with either birth weight or the instantaneous growth rate of fawns. Though compensatory growth was again displayed by light birth-weight fawns, they failed to reach weights equal to heavier-born fawns, at 25, 60 and 90 days of age. Saddleir (1980b) suggested that this might be due to either low protein values in the milk or to a genetic factor which governs similar growth rates over similar ages when dams and their fawns were compared.

The study reported here endeavored to describe quantitatively the patterns of suckling activity of captive, maternally raised black-tailed deer fawns from 24 h behavioral observations during the first 4 months of age; to describe the behavioral relationships between fawns and their dams in initiating and terminating suckling activities; and to investigate the relationships between fawn suckling behaviors and fawn birth weight, milk consumption and growth. Behavioral information of this type is necessary to more fully evaluate the

differences in fawn mortality and growth due to the sex of the fawns, the parity of the dam and the effects of milk supply when either twin or single fawns are nursed by their dams. In view of the work of Geist (1971), Horejsi (1972), Shackleton (1973) and Berger (1979) using suckling behavioral parameters in the field to assess differences in population quality of bighorn sheep (Ovis canadensis) and Stone sheep (O. dalli), these data may also be of use in field evaluations of black-tailed deer populations.

II. METHODS

Study Site

Observations of behavior were made in 1976 and 1977 at the deer research unit located in the University of British Columbia Research Forest, Maple Ridge, British Columbia. The research unit consists of a 1 ha fenced enclosure containing a small central circular building 4 m in diameter with a conical roof and a small holding paddock. Attached to the central building were 20 pie-wedge shaped holding pens, each 18.5 m, with an asphalt base and separated by a 2.44 m high chain-link fence. Does were placed in the pens 1 month prior to parturition. Each pen contained a sawdust covered bedding area and food and water containers. In 1977, jute sacking 2 m high was hung on the fence to prevent conspecifics in adjacent pens from seeing each other. Deer were protected from the weather by overhangs on the roof of the building. Topography and vegetation within the 1 ha enclosure have been described by Mueller (1977).

Study Animals

All black-tailed deer at the research unit were born in captivity and raised by their dams except for the original breeding members which were caught as fawns on Vancouver Island and hand-raised. Capture and rearing methods were presented by Mueller (1977). Prior to parturition all mature does were removed from the large compound and placed in the separate study pens. During each of the 2 years of the study, 5 does and their fawns were selected as observational animals based upon the closeness of their dates of parturition. Does varied in age, weight and past reproductive history (Table 1). With one exception, all does gave birth to healthy twin fawns with "normal" birth weights ranging from 2.20-3.24 kg (Mueller and Sadleir, 1980). In 1977, one doe gave birth to a healthy single female fawn, F2F, of "normal" birth weight and both dam and fawn were introduced to the study at 22 days post partum. In 1976, prior to the commencement of observations, one member from two sibling pairs was removed from the study for other research purposes and the remaining siblings were each raised by their dams as twin-born but single-raised fawns.

During both study years all does and fawns were maintained on calf starter pellets (4.196 kcal/g, 0.184 g crude protein/g), alfalfa hay (pelleted in 1977 and containing 4.352 kcal/g, 0.185 g crude protein/g) and water, ad libitum.

Table 1. The study animals.

Year	Fawn	Date of birth	Sex	Birth weight, kg	Immediate post partum weight of dam, kg	Age of dam, years	Previous number of fawns
1976							
	M18B	10.6.76	M	2.20	51.5	3	1
	M18C	"	M	2.50			
	MEB	13.6.76	M	2.50	37.7	2	1
	FEC	"	F	2.35			
	FFA	13.6.76	F	2.60	44.5	2	0
	MFB	"	M	2.35			
	F23E ¹	13.6.76	F	2.20	43.6	3	3
	F15E ¹	13.6.76	F	3.05	51.8	3	3
1977							
	M15F	20.6.77	M	3.24	60.9(0) ²	4	5
	M15G	"	M	3.18			
	M17BA	23.6.77	M	2.20	39.7(7)	2	0
	M17BB	"	M	2.50			
	M21AC	20.6.77	M	2.63	47.9(10)	3	2
	M21AD	"	M	2.48			
	FED	25.6.77	F	2.70	41.2(5)	3	3
	FEE ³	"	F	2.90			
	F2F ³	27.6.77	F	3.00	47.9(16)	4	5

¹ Born as twins, raised as singles.

² Day at which first post partum weight recorded for dam.

³ Single born, introduced to study at 22 days post-partum.

Behavioral Observations

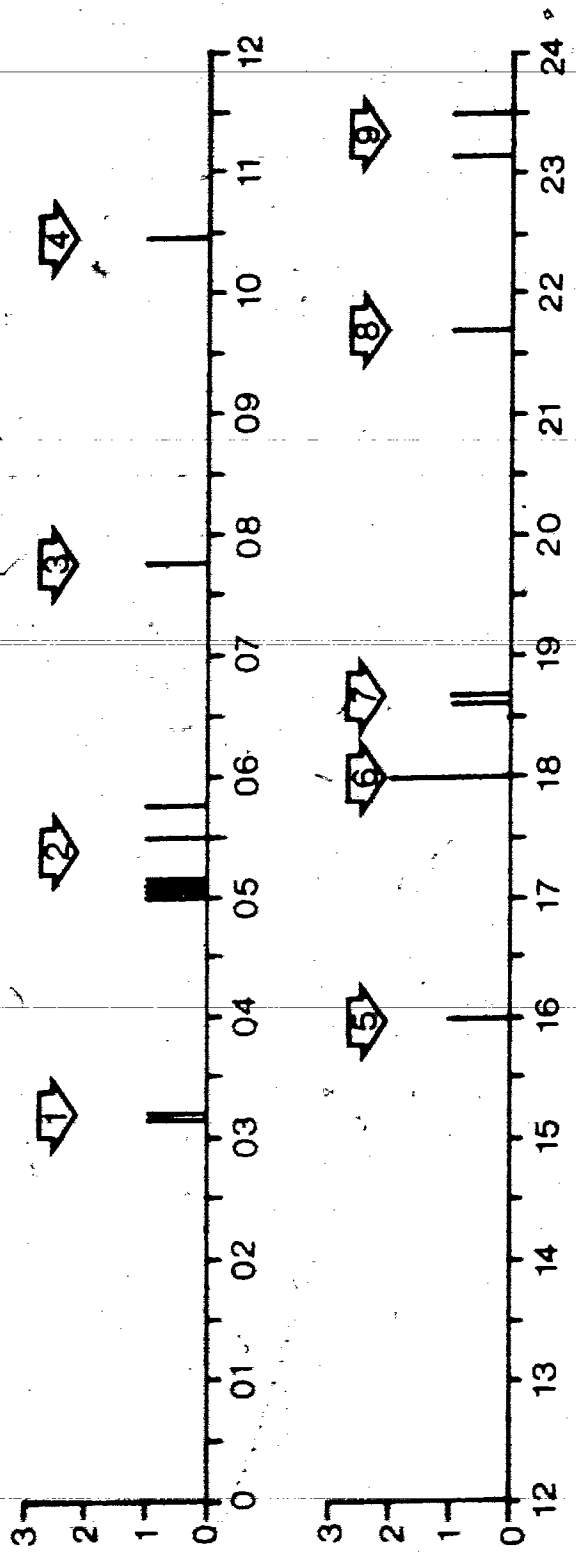
Behavioral Classifications

Preliminary observations on fawn suckling activity were conducted once fawning commenced but prior to the commencement of the study to define various behavioral characteristics of suckling.

Suckling has been defined by Cowie et al. (1951) as the activity of the young with the aim of obtaining milk from the mammary gland. Nursing has been defined by the same authors as the behavior of the dam which promotes access of the young to the teats. I have defined a suckling attempt as beginning each time a fawn placed its mouth upon the teat and ending when it relinquished the teat. A number of sequential suckling attempts constituted a suckling bout. Each suckling bout was defined as a period of time during which one or more suckling attempts occurred followed by a period of at least 30 minutes during which no suckling attempts were observed (Figure 1). This approach was adopted to distinguish individual suckling attempts from suckling bouts. Few authors have made this distinction making species comparisons difficult (Lent, 1974). Linsdale and Tomich

Figure 1. Distribution of suckling attempts of a single fawn (M18C - 29 days old) over a 24 h period grouped into suckling bouts using the criteria that a bout contains one or more suckling attempts and that bouts are temporally separated by a period of at least 0.5 h. Arrows numerically indicate each bout.

NUMBER OF SUCKLING ATTEMPTS



TIME OF DAY (in hours)

(1953) reported that suckling bouts in mule deer consisted of one or more suckling periods which last up to 1 h in length.

Langenau and Lerg (1976) and Faatz (1976) recorded individual suckling attempts in white-tailed deer but made no attempt to classify these attempts into bouts.

Since transfer of milk from dam to fawn constitutes a successful suckling attempt and is obviously difficult to determine by observation alone, a system of evaluating suckling success by behavioral criteria was developed and used.

Autenrieth and Fichter (1975) cite personal communications from D. Müller-Schwarze that black-tailed deer fawns wag their tails and exhibit a milk-kick with the front legs while suckling which may have a stimulating effect upon the dam to let-down milk. Tail wagging is a frequently observed behavior of suckling mule deer fawns (Linsdale and Tomich, 1953) and in suckling white-tailed deer fawns (Townsend and Bailey, 1975; Faatz, 1976; Langenau and Lerg, 1976). Langenau and Lerg (1976) suggested that tail wagging may serve to inhibit dams from terminating the nursing bout. Townsend and Bailey (1975) have suggested that tail wagging may act as a stimulus to inform a bedded fawn that its sibling is suckling and thereby attract it to also participate in suckling activities. The milk-kick occurs in suckling white-tailed deer fawns (Severinghaus and Gheatum, 1956) but is apparent only after suckling has been initiated (Faatz, 1976). White-tailed deer dams who are nursing exhibit a

hunched posture while standing (White et al., 1972; Faatz, 1976) which is characterized by a lowering of the haunches, arched back, forward extension of the neck and an apparent degree of semi-oblivion to surrounding events. Bunting, or prodding, of the dam's udder with the muzzle by suckling fawns stimulates milk let-down in mule deer (Linsdale and Tomich, 1953). A measure of suckling success in white-tailed deer fawns was reported by Langenau and Lerg (1976) to be any suckling attempt greater than 5 s.

In this study suckling attempts were recorded as being successful when one or more of the following behaviors were exhibited while fawns were in contact with the teat: tail wagging of fawns; anal licking of fawns by dams; hunched nursing posture of dams; foreleg milk-kick of fawns; udder bunting by fawns; and teat contact greater than 5 s on the initial suckling attempt. If contact with the teat was broken after suckling had been successfully initiated but was resumed quickly, such as by the fawn changing teats or pausing to breathe, this second attempt was also considered successful provided at least one of the above behavioral criteria were met.

The duration of each successful suckling attempt was recorded in seconds as the duration of time that the fawn was in constant contact with the teat during the attempt.

Unsuccessful suckling attempts were recorded as being either shorter than 5 s in duration, or not exhibiting either

tail wagging, milk kicking and udder bunting by fawns or anal licking and nursing posture by dams.

Individual suckling attempts were further classified by the initiator and terminator, either fawn or dam. Suckling attempts initiated by dams were identified by vocalizing, walking and licking behavior. Vocalizing occurred occasionally when dams emitted a low grunt to distract fawns from sleep or other activity, which resulted in a suckling attempt. Following bedding periods the dam would rise, stretch and move about the pens, attracting the attention of her fawns so that they would then rise from their bedding sites, approach the dam and attempt to suckle. Often a dam would approach and vigorously lick her fawns, usually around the anal-genital area, which resulted in suckling attempts by the fawns. Fawn initiations of suckling attempts were identified by either vocalizing, teat seeking, or tail wagging behaviors. Fawns would occasionally emit a low whine call resulting in grooming by the dam and subsequent suckling. Teat seeking behavior was exhibited by fawns when they either arose from a bedded position, ceased feeding on solid food, or ceased playing and went directly to the dam and began suckling without any apparent external cues. Teat seeking was also used to classify suckling attempts which were quickly resumed following the fawn breaking contact with the teat. When a fawn arose from its bedding site, approached its dam and suckled while its sibling was suckling and wagging its tail, the

attempt was classified as being initiated by the tail wagging stimulus of the suckling sibling as suggested by Townsend and Bailey (1975).

Do terminations of fawn suckling attempts were characterized by the dam either lifting her hind leg and stepping over the suckling fawn, or by pushing the fawn away from the teat with her head or hind leg, or by lying down, or by jumping away from an aggressively bunting fawn. Fawns terminated suckling attempts either by walking away from the dam apparently satiated, or by breaking contact with the teat to either rest or breathe, or by dropping or crouching down into a prone position due to sudden disturbances, or by antagonism between fawns while suckling. The latter occurred very infrequently and only when siblings suckled simultaneously and aggressively from the same flank of the dam. This occurred when one fawn shifted its position without releasing the teat which caused the other fawn to break contact with the teat. It was noted that both initiation and termination of suckling were occasionally triggered by various disturbances occurring either inside or outside of the research unit such as human activity, loud noises and aircraft.

Observational Recording

Behavioral observations were conducted continuously over a 24 h period from inside the round central building housing the attached individual study pens. Five adjacent pens, each equipped with a clear 46 X 100 cm plexiglass door and a 15 watt overhead incandescent lamp to permit nocturnal viewing, were used. Observers sitting quietly 1.6 to 2.0 m from the doors in the centre of the room had a clear field of vision of all pens (Figure 2). All fawns were ear tagged at birth with plastic tags ("Lone Star", Y-TEX Corporation, Cody, Wyoming) bearing identification codes. Prior to 24 h observations one fawn of each sibling pair was tagged with fluorescent colored forestry flagging tape about the neck with streamers that dangled to the ground.

Suckling durations were timed by hand held stop watches ("Herwins Super Hattrick", Edwin Schlup, Switzerland) calibrated to 0.2 s. Behavioral data on suckling attempts were written on individual fawn charts and included time of day, suckling durations, initiator and terminator, success or non-success, orientation of fawn to dam and nursing position of dam. Also recorded were items other than milk ingested by fawns.

During the first year of the study 2 observers were employed each working alone on 8 h observation shifts. During the second year 6 observers were employed each working 4 h

Figure 2. Observer's view of the study animals from inside the circular barn. Three of the 5 pens are shown with the clear plexiglass doors removed for clarity.



on and 8 h off with 2 observers on at all times thus allowing one observer to watch 4 fawns and the other, 5 fawns. Shift starts were staggered 2 h apart. All observers were thoroughly trained in each of the years to reduce error and minimize bias. Observer fatigue was minimized with 8 h rest periods between shifts.

Weight Determinations and Milk Consumption

Holding pens were checked daily for newborn fawns and birth weights were recorded after the fawns were licked dry by their dams. In 1976, fawns were weighed each day during the first 40 days of age and weekly thereafter on a platform scale (Health-O-Meter, Continental Scale Corporation, Chicago, Illinois) with a maximum capacity of 160 kg in 0.1 kg graduations. In 1977, fawns were weighed free-standing on an electronic platform scale (Western Scale Ltd., Port Coquitlam, B.C.) at weekly intervals. Weight on the scale platform was transmitted to a single strain gauge whose output was converted to a digital readout. The scale weighed to 40 kg in 2 g units and to 80 kg in 4 g units. Weights of moving fawns were electronically averaged from 10 weights taken at 0.33 second intervals. The scale rested on a concrete pad, surrounded by a wooden enclosure with doors at either end to facilitate fawn entry and exit.

Milk consumption by fawns was measured in 1977 only, during a 24 h period immediately following the 24 h behavioral observations. Consumption was measured in 6 twin fawns using a weight transfer method (Sadleir, 1980a,b) in which diapered fawns were weighed before and after introduction to their dams. The frequency of milk consumption measurements declined as fawns increased in age from 12/day in the first week to 3/day at 4 months. The frequency and duration of fawn suckling activity and the behavioral measure of success for each suckling attempt were recorded while both fawns were with their dam, suckling and consuming milk. The dates of behavioral observations, milk consumption trials, and the number of fawns observed are presented in Table 2.

Data Analysis

Suckling behaviors from 24 h observation periods were identified and recorded, and daily totals of each behavior were calculated for each fawn at intervals throughout the first 4 months of age. Since behavioral observations were conducted on fawns born in 2 consecutive years behavioral data were separated into year classes. Quantitative changes in behavior types exhibited by the fawns in each year class were assessed in numerous ways as fawns increased in age from birth.

1. The measurements of each type of behavior were first pooled

Table 2. Dates of behavioral observations and milk consumption trials and numbers of fawns observed by year.

1976		1977	
Date	# Fawns observed	Date	# Fawns observed
14.06.76	8	28.06.77	8
22.06.76	8	29.06.77 *	6
28.06.76	8	05.07.77	8
05.07.76	6	06.07.77 *	6
13.07.76	6	12.07.77	8
19.07.76	6	13.07.77 *	6
03.08.76	8	19.07.77	9
30.08.76	8	27.07.77 *	6
		02.08.77	9
		16.08.77	9
		17.08.77 *	6
		13.09.77	9
		14.09.77 •	6
		19.10.77	6
		20.10.77 •	6

* Dates at which behavioral observations were made during milk consumption trials.

by year into fawn age groups (Table 3) and the mean frequencies and durations of each behavior by age group were then calculated. When age groups were considered, 1977 fawns were found to be significantly younger than 1976 fawns in the youngest age group and, significantly older than 1976 fawns in the 60-89 day age group (Mann-Whitney rank test). No significant differences in fawn age between years were found for any other age groupings. The average behavior values between years inside each age group were then compared using two sample nonparametric Mann-Whitney rank tests.

2. Natural logarithm transformations of individual suckling behaviors for both an all-fawn and an all-twin fawn group over all ages by sample year were performed to achieve normality, homoscedasticity and linearity. Simple linear regression equations of lognormal transformations of each measure of behavior against age were derived for both the all-fawn and all-twin fawn groups. Similarly, regression equations were calculated for each suckling behavior within each year for the following 4 groups of fawns: males and females; twins and singles; fawns of primiparous and pluriparous dams; and fawns with birth weights arbitrarily classed into 3 weight groups, ie. 2.00-2.49 kg, 2.50-2.99 kg and 3.00-3.49 kg. A t-test of regression equation slopes was used to determine if the slopes differed significantly from

Table 3. Mean age of fawns in each age group for each year.

		Age of fawns (days)						
		0-9	10-19	20-29	30-39	40-59	60-89	90+
1976	\bar{x}	9.00	15.00	23.00	34.00	51.75	78.75	—
	S.E.	0.00	0.63	0.63	1.00	0.49	0.49	—
	n ^a	6	10	6	12	8	8	—
1977	\bar{x}	6.00	14.67	25.08	37.33	49.47	82.44	120.00
	S.E.	0.80	0.85	0.85	0.67	1.73	0.90	0.63
	n ^a	8	12	13	3	15	9	6
U ^b		48.00 *	62.00	56.00	28.00	62.00	66.00 *	

^a Number of fawns.

^b Mann-Whitney rank test statistic between years.

* Means significantly different between years, $P \leq 0.05$.

zero. Both between year and within year comparisons of regression equation slopes and y-intercepts were performed using an analysis of covariance procedure (Zar, 1974). Between year comparisons were used to determine whether the data collected in each year came from the same population. Within year comparisons were used to detect more subtle behavioral differences between sex, number of siblings, dam parity and birth weights of fawns. The resultant statistics generated by this analysis were F_a for comparing the y-intercepts of regressions and F_b for comparing the slopes of regressions. Regression equations in either the form $\ln(Y)=a+bX$ or $\ln(Y+1)=a+bX$ are presented and estimates of average behavior characteristics (Y) at any age (X) were derived from back transformed regressions in either the form $Y=\exp(a+bX)$ or $Y=\exp(a+bX)-1$

3. Two sample nonparametric Mann-Whitney rank tests were again employed to compare the variability of behaviors both within year and between year age groups. This method was used when treating the following behaviors:
 - a. the number of individual suckling bouts/fawn/24 h which were initiated by either the dam or the fawn;
 - b. the number of individual suckling attempts/fawn/24 h which were either initiated or terminated by either the dam or the fawn; and,
 - c. the number of individual suckling attempts/fawn/24 h

which were either initiated and terminated by the dam; initiated and terminated by the fawn; initiated by the dam and terminated by the fawn; or, initiated by the fawn and, terminated by the dam.

4. In 3(c) above, where behaviors were grouped into 4 categories, a nonparametric analysis of variance by ranks was performed using the Kruskal-Wallis rank test, corrected for tied ranks, to determine intergroup differences.
5. Comparisons of suckling behaviors with fawn growth, weights and milk consumption, were performed using only the data on twin fawns pooled from both year samples and employed the following analytical techniques:
 - a. Weights of 1977 twin fawns were interpolated to their ages on the observation dates from known weekly weights using a cubic polynomial regression procedure (Yu, 1978).
 - b. Since solid food intake by fawns is negligible until after 25 days of age (Sadleir, 1980b), instantaneous growth rates at the observation date closest to 25 days of age were calculated for twin fawns on a milk diet in both years using the equation suggested by Brody (1964) in the form $k = (\ln W_2 - \ln W_1) / (t_2 - t_1)$ where: k is the instantaneous growth rate on the day of measurement; \ln is the natural logarithm; W_2 is the weight on the observation date nearest 25 days of age; W_1 is the birth

weight; t_2 is the age on the observation date; and, t_1 is the age at birth (zero).

- c. Rates of weight gain of twin fawns in each year to 24 days of age were calculated using a comparison of simple linear regression equation slopes of lognormal weights regressed against age. These comparisons used an analysis of covariance procedure (Zar, 1974). Weights to 24 days of age used in this calculation were actual weights, rather than interpolated weights.
- d. Totals for each of the 5 suckling behaviors of twin fawns from birth to the observation date closest to 25 days of age were estimated by integration and least squares interpolation of the known behavioral values from birth to the observation date. Behavioral values recorded on the first observation date were used as estimates of behavior from birth and were included in the integration. Average daily suckling behavioral estimates from birth to 25 days of age were calculated by dividing total suckling behavior estimates from the integration by the age on the observation date.
- e. Variability between sample years of birth weights, the weights, ages and instantaneous growth rates on the observation date nearest 25 days and, the daily suckling behaviors from birth to this observation date were compared using two sample nonparametric Mann-Whitney

rank tests.

- f. Simple linear regressions of the average daily suckling behaviors to 25 days of age against both instantaneous growth rates at 25 days and birth weight were performed and, simple correlation coefficients determined to show the significance of these relationships. Similarly, instantaneous growth rates at 25 days were regressed against birth weights and correlation coefficients calculated.
- g. Total milk consumption (g)/fawn/24 h during the first 25 days of age and from birth to 60 days were estimated by integration and least squares interpolation of absolute total milk consumption during milk consumption trials from birth (Sadleir, 1980b). Daily milk consumptions prior to the first measurements were assumed to be the same from birth to the first measurement and were used in the integration. Simple linear regression analyses of total estimated milk consumption on birth weight were performed and simple correlation coefficients calculated for fawns in each of 2 age groups: 0-25 days and 0-60 days. Absolute milk consumption(g)/fawn/24 h was similarly regressed against absolute suckling duration(min)/fawn/24 h for each consumption trial up to 121 days of age and correlation coefficients were calculated. Rates of milk intake(g/s) while suckling, or

the suckling efficiency, were calculated by dividing the absolute milk consumption(g)/fawn/24 h by the absolute suckling duration(s)/fawn/24 h.

Statistical Significance

Statistical significance was determined at $P \leq 0.05$, using two-tailed tests.

III. RESULTS

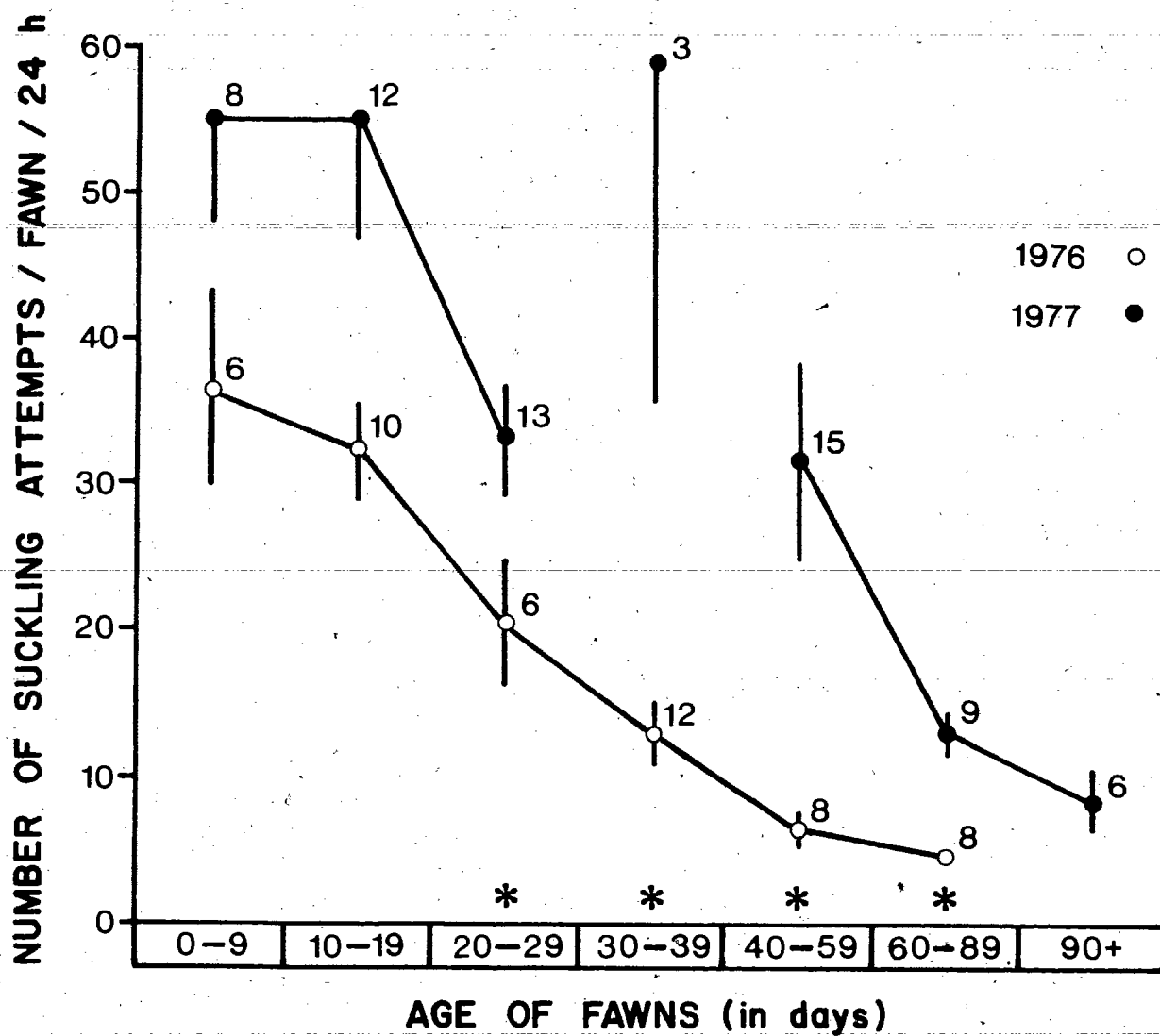
Changes in Suckling Behavior with Increasing Age

Five suckling behaviors were identified and compared with changes in age. These were identified and abbreviated as follows:

- a. total number of suckling attempts/fawn/24 h, NA;
 - b. total number of successful suckling attempts/fawn/24 h, NSA;
 - c. total duration of successful suckling attempts/fawn/24 h, in minutes, DSA;
 - d. total number of suckling bouts/fawn/24 h, NB; and,
 - e. total number of suckling bouts/fawn/24 h with one, or more, successful suckling attempts, NSB.
-
1. Total numbers of suckling attempts/fawn/24 hours, NA.

The pattern of NA was found to decline with increasing fawn age (Figure 3). Between year comparisons of NA by age groups showed that no significant differences existed between years during both the 0-9 and 10-19 day age groups.

Figure 3. Changes in the mean number of suckling attempts/fawn/24 h with increasing age ($\bar{x} \pm \text{S.E.}$). All observed fawns considered. Statistical significance of \bar{x} between years within each age group indicated by asterisk ($P \leq 0.05$). Sample sizes indicated at \bar{x} .



In all age groups after 19 days 1977 fawns exhibited significantly greater NA than 1976 fawns. Although the general trend in NA declined as fawns grew older, considerable individual variation in this behavior was displayed in each age group during both years. For example within the 0-9 day age group NA ranged from 15-56 in 1976 and from 15-83 in 1977 and, from 60-89 days of age NA ranged from 3-7 in 1976 and from 8-21 in 1977.

Between year comparisons of $\ln NA$ regressed against age resulted in regression equations for 1977 fawns having both significantly higher y-intercept and lower slope values than 1976 fawns in both the all-fawn and all-twin fawn categories (Table 4). Because of the significantly different slopes and intercepts found between years all subsequent comparisons of this behavior were carried out on within year samples only.

The slope of the regression equations represents the real average rate of decline in behavioral frequency over all ages. Greater slope values represent steeper slopes. The y-intercept represents the average behavioral frequency on the day of birth but is a somewhat misleading estimate because the youngest fawns observed in 1976 and 1977 were 9 and 3 days old, respectively. Intercept values are necessary for the statistical comparisons of regression equations.

Observational data for 1976 and 1977 fawns were collected over 81 and 121 days post partum, respectively.

Table 4. Summary of test statistics derived from between group comparisons of simple linear regression equations of \ln (number of suckling attempts per fawn per 24 hours) on age. Statistical significance measured at $P < 0.05$. Regression equations in the form $\ln(Y) = a + bX$. Back transformed regressions may be calculated in the form $Y = \exp(a + bX)$.

	N^1	n^2	a	$b \pm S.E._b$	t_b	r	F_a^3	F_b^4
1976 Fawns	8	50	3.6658	-0.0305 \pm 0.0029	-10.493 *	-0.834 *	81.35 *	14.74 *
1977 Fawns	9	66	4.0451	-0.0170 \pm 0.0018	-9.320 *	-0.758 *		
1976 Twins	6	36	3.8791	-0.0350 \pm 0.0031	-11.106 *	-0.885 *	61.65 *	22.26 *
1977 Twins	8	62	4.0722	-0.0169 \pm 0.0018	-9.284 *	-0.767 *		
1976 Fawns:								
Twins	6	36	3.8791	-0.0350 \pm 0.0031	-11.106 *	-0.885 *	1.36	7.68 *
Twins raised as singles	2	14	3.1009	-0.0177 \pm 0.0053	-3.336 *	-0.693 *		
Males	4	25	3.8774	-0.0346 \pm 0.0043	-8.012 *	-0.858 *	0.74	2.00
Females	4	25	3.4677	-0.0265 \pm 0.0038	-6.942 *	-0.822 *		
Of Primiparous Dams	2	8	4.1850	-0.0431 \pm 0.0052 *	-8.242 *	-0.958 *	0.05	6.34 *
Of Pluriparous Dams	6	42	3.5221	-0.0266 \pm 0.0032	-8.257 *	-0.793 *		
By Birth Weight Classes								
2.00 - 2.49 kg	4	25	3.5044	-0.0281 \pm 0.0044	-6.265 *	-0.794 *		
2.50 - 2.99 kg	3	18	3.9759	-0.0360 \pm 0.0046	-7.752 *	-0.888 *	0.77	1.146
3.00 - 3.49 kg	1	7	3.4341	-0.0241 \pm 0.0045	-5.352 *	-0.922 *		
1977 Fawns:								
Twins	8	62	4.0722	-0.0169 \pm 0.0018	-9.284 *	-0.767 *	4.11	0.001
Singles	1	4	3.5819	-0.0175 \pm 0.0111	-1.573	-0.743		
Males	6	48	3.8485	-0.0150 \pm 0.0014	-10.035 *	-0.828 *	8.10 *	3.25
Females	3	18	4.5520	-0.0237 \pm 0.0063	-3.727 *	-0.681 *		
Of Primiparous Dams	2	16	3.8418	-0.0171 \pm 0.0026	-6.392 *	-0.863 *	3.77	0.004
Of Pluriparous Dams	7	50	4.1061	-0.0169 \pm 0.0022	-7.551 *	-0.736 *		
By Birth Weight Classes								
2.00 - 2.49 kg	2	16	3.7070	-0.0132 \pm 0.0029	-4.570 *	-0.773 *		
2.50 - 2.99 kg	4	30	4.3001	-0.0206 \pm 0.0031	-6.508 *	-0.775 *	1.70	1.71
3.00 - 3.49 kg	3	20	3.8907	-0.0146 \pm 0.0028	-5.149 *	-0.771 *		

¹Number of Individual Fawns

²Number of Observations

³F-test comparing intercepts of regression

⁴F-test comparing slopes of regression

* Significant, $P \leq 0.05$

Within the 1976 sample, twin-raised fawns exhibited significantly steeper slopes of $\ln NA$ with age than 2 twin-born but single-raised fawns although their intercepts were not significantly different. There were no differences in the regressions of male and female fawns. Although the numbers of observations were few, the twin fawns of a primiparous dam exhibited significantly steeper regression slopes than the fawns of pluriparous dams but no significant differences were found in the intercept values of their regression equations. Fawns of different birth-weight classes in 1976 showed no significant differences in their regression equations.

Within the 1977 sample the only significant differences found in the regression equations was that male fawns showed lower intercept values of their $\ln NA$ than females.

With the exception of a single-born female fawn in 1977, introduced to the study at 22 days of age, all fawn groups in both years exhibited significant negative slopes not equal to zero and significant negative correlations of $\ln NA$ with age.

2. Total numbers of successful suckling attempts/fawn/24 hours, NSA.

The pattern of NSA was found to decline as fawns increased in age (Figure 4). Between year comparisons of NSA by age groups showed that 1977 fawns exhibited significantly greater NSA during both the 20-29 day and the 40-59 day age groups. No significant differences in NSA were found between years during any other age groups. In age groups where significant differences in NSA were found, fawn ages between years were not significantly different. Considerable individual variation in NSA was found between fawns in each age group in each year. In both years suckling attempts were never 100 percent successful in any age group when the data for all fawns were pooled. However, a few individuals were successful in all attempts but only after 60 days of age.

Between year comparisons of $\ln(\text{NSA} + 1)$ regressed against age, resulted in regression equations for 1977 fawns having significantly higher intercepts than 1976 fawns in both the all-fawn and all-twin fawn categories (Table 5). No significant difference between the slopes of the regression equations in each of these groups were found. Because of the significantly different regression equations found between years, all subsequent comparisons were carried out on within year samples only.

Figure 4. Changes in the mean number of successful suckling attempts/fawn/24 h with increasing age ($\bar{x} \pm$ S.E.). Legend as for Figure 3.

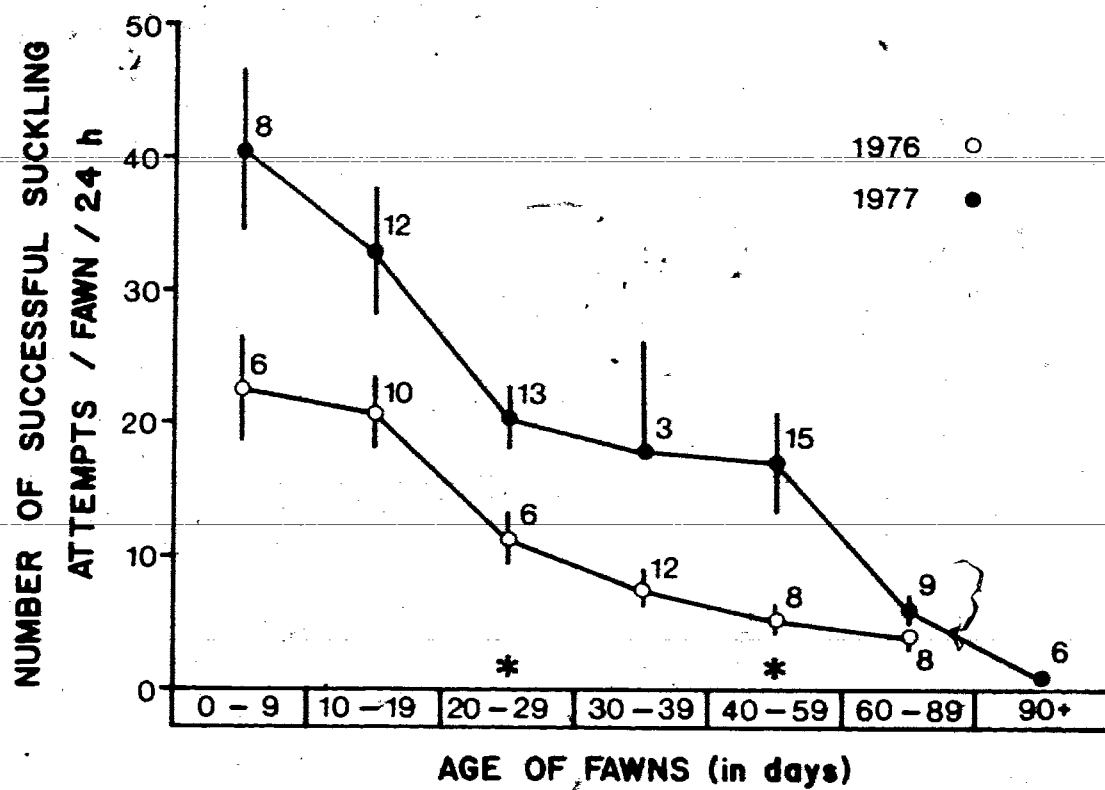


Table 5. Summary of test statistics derived from between group comparisons of simple linear regression equations of \ln (number of successful suckling attempts + 1 per fawn per 24 hours) on age. Statistical significance measured at $P \leq 0.05$. Regression equations in the form $\ln(Y + 1) = a + bX$. Back transformed regressions may be calculated in the form $Y = \exp(a + bX) - 1$.

	N^1	n^2	a	$b \pm S.E.b$	t_b	r	P_a^3	F_b^4
1976 Fawns	8	50	3.1312	-0.0223 \pm 0.0025	-8.781 *	-0.785 *	38.83 *	0.017
1977 Fawns	9	66	3.7104	-0.0228 \pm 0.0018	-12.042 *	-0.832 *		
1976 Twins	6	36	3.2216	-0.0247 \pm 0.0030	-8.150 *	-0.813 *	44.12 *	0.32
1977 Twins	8	62	3.7735	-0.0227 \pm 0.0017	-13.367 *	-0.865 *		
1976 Fawns:								
Twins	6	36	3.2216	-0.0247 \pm 0.0030	-8.150 *	-0.813 *	0.002	2.71
Twins Raised As Singles	2	14	2.8808	-0.0152 \pm 0.0044	-3.441 *	-0.704 *		
Males	4	25	3.2028	-0.0236 \pm 0.0039	-5.970 *	-0.779 *	0.14	0.25
Females	4	25	3.0644	-0.0210 \pm 0.0033	-6.327 *	-0.796 *		
Of Primiparous Dams	2	8	3.5211	-0.0343 \pm 0.0047	-7.225 *	-0.947 *	0.25	7.77 *
Of Pluriparous Dams	6	42	3.0104	-0.0185 \pm 0.0027	-6.724 *	-0.728 *		
By Birth Weight Classes								
2.00 - 2.49 kg	4	25	3.0145	-0.0208 \pm 0.0037	-5.515 *	-0.754 *		
2.50 - 2.99 kg	3	18	3.2865	-0.0256 \pm 0.0044	-5.748 *	-0.820 *	0.72	0.56
3.00 - 3.49 kg	1	7	3.1242	-0.0181 \pm 0.0040	-4.455 *	-0.893 *		
1977 Fawns:								
Twins	8	62	3.7735	-0.0227 \pm 0.0017	-13.367 *	-0.865 *	21.55 *	0.19
Singles	1	4	2.4554	-0.0177 \pm 0.0042	-4.154	-0.946		
Males	6	48	3.5874	-0.0213 \pm 0.0015	-14.064 *	-0.900 *	2.01	1.82
Females	3	18	4.0573	-0.0284 \pm 0.0074	-3.848 *	-0.693 *		
Of Primiparous Dams	2	16	3.2381	-0.0173 \pm 0.0022	-7.675 *	-0.898 *	4.37	3.32
Of Pluriparous Dams	7	50	3.8697	-0.0247 \pm 0.0023	-10.767 *	-0.840 *		
By Birth Weight Classes								
2.00 - 2.49 kg	2	16	3.4734	-0.0215 \pm 0.0033	-6.368 *	-0.862 *		
2.50 - 2.99 kg	4	30	3.8488	-0.0227 \pm 0.0028	-7.843 *	-0.828 *	2.32	0.04
3.00 - 3.49 kg	3	20	3.6404	-0.0227 \pm 0.0036	-6.2344 *	-0.826 *		

¹Number of Individual Fawns

²Number of Observations

³F-test comparing intercepts of regression

⁴F-test comparing slopes of regression

* Significant, $P \leq 0.05$

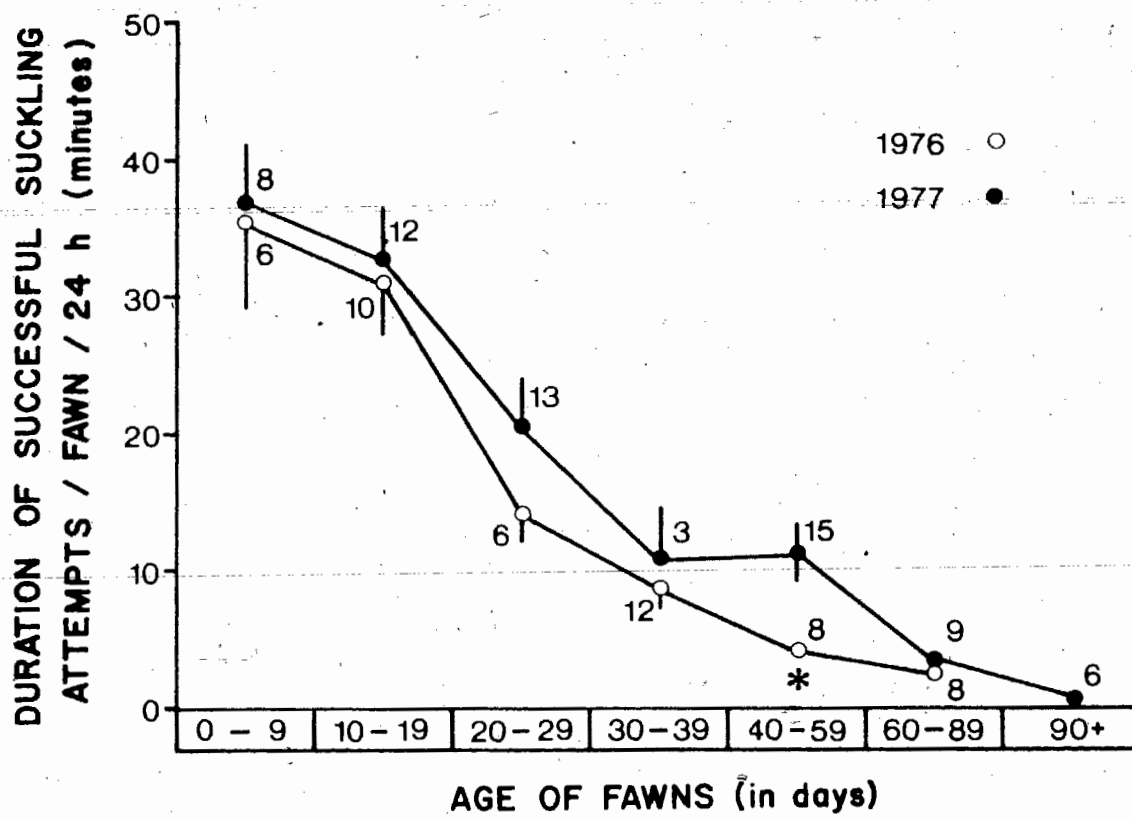
Within the 1976 sample no significant differences were found between any regression equations except that the fawns of primiparous dams exhibited significantly steeper slopes than fawns of pluriparous dams but had non-significant differences of intercepts.

Within the 1977 sample, with the possible exception of the twin and single fawns, no significant differences in regression equations of $\ln(\text{NSA} + 1)$ were found for any of the fawn groups. However, any real differences between the behaviors of single and twin fawns were inconclusive as the requirements for a valid regression equation representing the behavior of the single fawn were not met. A lack of significance in both the slope, t_b , and the correlation coefficient, r , for this single-born animal may be entirely due to limited behavioral data for it. This fawn was introduced to the study at 22 days of age and was observed for only 4 24 h periods.

3. Total duration of successful suckling attempts/fawn/24 hours, in minutes, DSA.

The pattern of DSA was found to decline as fawns increased in age (Figure 5). Between year comparisons of DSA by age groups showed that no significant differences existed

Figure 5. Changes in the mean duration of successful suckling attempts/fawn/24 h with increasing age ($\bar{x} \pm \text{S.E.}$). Legend as for Figure 3.



between years, except for the 40-59 day age interval. Within this age group, 1977 fawns exhibited significantly greater DSA than 1976 fawns. DSA varied considerably between individual fawns in each of the age groups during both years. For example, during the first 9 days of age DSA ranged from 20.48-55.88 min in 1976 and from 20.15-53.17 min in 1977 while within the 60-89 day age group DSA ranged from 1.28-3.75 min in 1976 and from 1.23-4.75 min in 1977.

Between year comparisons of $\ln(\text{DSA} + 1)$ regressed against age resulted in regression equations in which 1977 fawns had significantly higher intercepts than 1976 fawns and, in both years the slopes were similar (Table 6). When only twin fawns in each year were considered in the regressions, the equations for 1976 twins had significantly higher intercepts and significantly steeper slopes than those of 1977 twin fawns. Although the intercept values in Table 6 appear numerically similar for both years in each of the all-fawn and all-twin fawn groups, DSA differences between years were significantly different. For example, intercept DSA values, when back transformed, were 39.90 min and 37.06 min for 1977 and 1976 fawns, respectively. Similarly, twin 1976 fawns had DSA values of 44.92 min compared to 42.83 min for 1977 twins at the intercept. Because of the significantly different regression equations found in between year comparisons, all subsequent analyses

Table 6. Summary of test statistics derived from between group comparisons of simple linear regression equations of \ln (duration of successful suckling attempts + 1 per fawn per 24 hours) on age. Statistical significance measured at $P \leq 0.05$. Regression equations in the form $\ln(Y + 1) = a + bX$. Back transformed regressions may be calculated in the form $Y = \exp(a + bX) - 1$, where Y is in minutes.

	N^1	n^2	a	$b \pm S.E.b$	t_b	r	F_a^3	F_b^4
1976 Fawns	8	50	3.6391	-0.0347 \pm 0.0028	-12.234 *	-0.870 *	13.20 *	4.09
1977 Fawns	9	66	3.7111	-0.0278 \pm 0.0017	-15.697 *	-0.890 *		
1976 Twins	6	36	3.8269	-0.0381 \pm 0.0031	-12.033 *	-0.899 *	13.20 *	8.95 *
1977 Twins	8	62	3.7803	-0.0279 \pm 0.0015	-18.130 *	-0.919 *		
1976 Fawns:								
Twins	6	36	3.8269	-0.0381 \pm 0.0031	-12.033 *	-0.899 *	2.43	4.25
Twins Raised As Singles	2	14	3.1531	-0.0253 \pm 0.0051	-4.879 *	-0.815 *		
Males	4	25	3.8157	-0.0369 \pm 0.0040	-9.169 *	-0.886 *	2.27	0.50
Females	4	25	3.4768	-0.0329 \pm 0.0039	-8.325 *	-0.866 *		
Of Primiparous Dams	2	8	4.1481	-0.0476 \pm 0.0061	-7.778 *	-0.953 *	0.008	7.07 *
Of Pluriparous Dams	6	42	3.4953	-0.0307 \pm 0.0030	-10.109 *	-0.847 *		
By Birth Weight Classes								
2.00 - 2.49 kg	4	25	3.5744	-0.0346 \pm 0.0043	-8.012 *	-0.858 *		
2.50 - 2.99 kg	3	18	3.8741	-0.0387 \pm 0.0047	-8.225 *	-0.899 *	0.53	1.32
3.00 - 3.49 kg	1	7	3.2464	-0.0236 \pm 0.0039	-6.061 *	-0.938 *		
1977 Fawns:								
Twins	8	62	3.7803	-0.0279 \pm 0.0015	-18.130 *	-0.919 *	26.90 *	1.02
Singles	1	4	2.2017	-0.0176 \pm 0.0010	-16.114 *	-0.996 *		
Males	6	48	3.6540	-0.0266 \pm 0.0015	-17.370 *	-0.931 *	0.005	2.37
Females	3	18	3.9496	-0.0344 \pm 0.0066	-5.161 *	-0.790 *		
Of Primiparous Dams	2	16	3.5698	-0.0276 \pm 0.0017	-16.187 *	-0.974 *	1.56	0.002
Of Pluriparous Dams	7	50	3.7544	-0.0278 \pm 0.0023	-12.059 *	-0.867 *		
By Birth Weight Classes								
2.00 - 2.49 kg	2	16	3.5414	-0.0268 \pm 0.0022	-11.799 *	-0.953 *		
2.50 - 2.99 kg	4	30	3.7910	-0.0282 \pm 0.0025	-11.149 *	-0.903 *	0.73	0.05
3.00 - 3.49 kg	3	20	3.7067	-0.0276 \pm 0.0043	-6.358 *	-0.831 *		

¹ Number Of Individual Fawns

² Number of Observations

³ F-test comparing intercepts of regression

⁴ F-test comparing slopes of regression

* Significant, $P \leq 0.05$

were carried out on within year samples only.

Within the 1976 sample no significant differences were found between any regression equations except that the fawns born to primiparous dams had similar intercept values of DSA but significantly steeper slopes when compared to fawns of pluriparous dams.

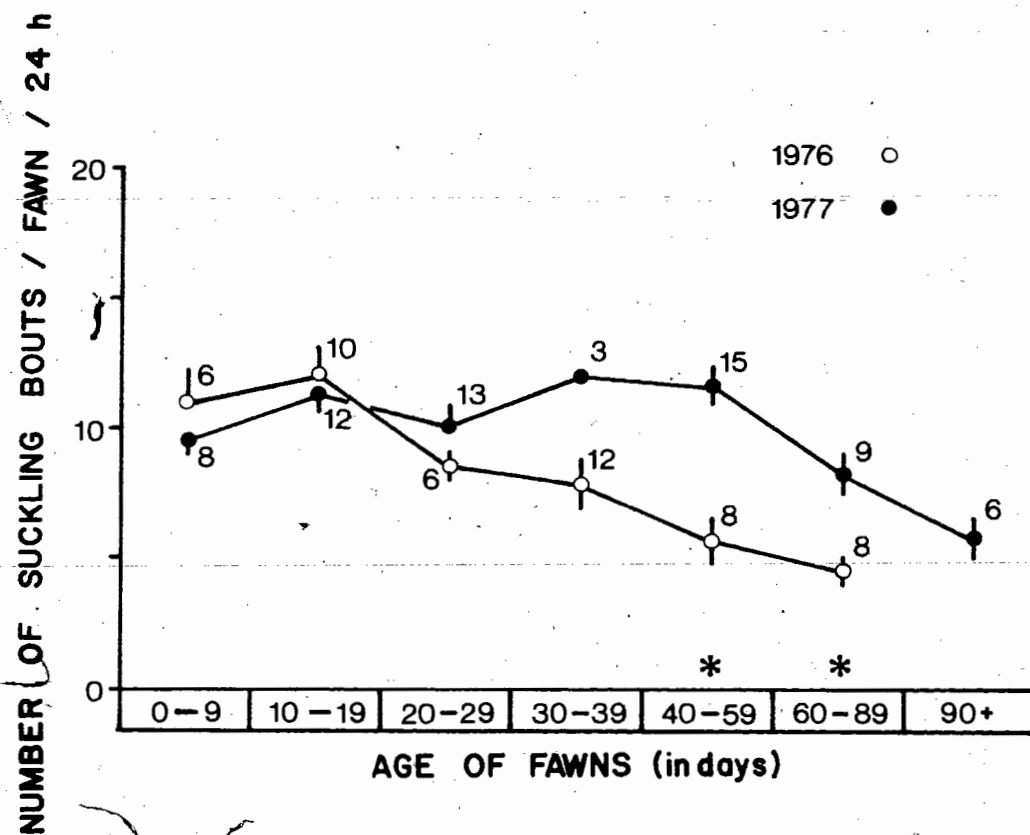
With the exception of the 1977 twin and single fawns no significant differences were found between regression equations for DSA. Both equations for twin and single fawns exhibited similar slopes but twin fawns exhibited significantly higher intercept values than the single-born fawn.

All regression equations of $\ln(\text{DSA} + 1)$ demonstrated significant negative correlations with increasing age of fawns and all equations had significant negative slopes not equal to zero.

4. Total number of suckling bouts/fawn/24 hours, NB.

The pattern of NB was found to decline as fawns grew older (Figure 6). This decline was most notable when data for individual fawns were compiled for specific ages rather than for pooled age groups. No significant differences in NB were found between years in age groups up to 39 days of age.

Figure 6. Changes in the mean number of suckling bouts/fawn/24 h with increasing age ($\bar{x} \pm$ S.E.). Legend as for Figure 3.



After 40 days, 1977 fawns exhibited significantly higher NB than 1976 fawns in each age group.

Between year comparisons of regression equations of $\ln \text{NB}$ regressed against age resulted in both 1976 fawns and 1976 twin fawns exhibiting significantly higher intercept values and significantly steeper slopes than either the 1977 fawns or the 1977 twin fawns (Table 7). The decline in NB appeared to be quite gradual. Back transformed regressions at 15, 30, 60 and 80 days showed that 1976 fawns on average exhibited 10, 8, 5 and 4 NB compared to 11, 10, 9, and 8 NB for 1977 fawns of the same ages. Similarly, at these ages 1976 twins on average exhibited 11, 8, 5 and 4 NB while 1977 twins exhibited NB unchanged from that of all the 1977 fawns. The biological significance of these statistical differences between regression equations for NB in each year appears to be quite slight. However, because of the significant statistical differences between regression equations for each sample year, all subsequent analyses were carried out on within year samples only.

Within the 1976 sample no significant differences were found between any regression equations except that the fawns born to primiparous dams exhibited steeper regression slopes than fawns born to pluriparous dams but had non-significant intercepts.

Table 7. Summary of test statistics derived from between group comparisons of simple linear regression equations of \ln (number of suckling bouts per fawn per 24 hours) on age. Statistical significance measured at $P \leq 0.05$. Regression equations in the form $\ln(Y) = a + bX$. Back transformed regressions may be calculated in the form $Y = \exp(a + bX)$.

	N^1	n^2	a	$b \pm S.E._b$	t_b	r	F^3_a	F^4_b
1976 Fawns	8	50	2.5484	-0.0145 ± 0.0018	-8.133 *	-0.761 *	23.24 *	23.24 *
1977 Fawns	9	66	2.4597	-0.0046 ± 0.0010	-4.376 *	-0.479 *		
1976 Twins	6	36	2.6132	-0.0162 ± 0.0021	-7.715 *	-0.798 *	20.30 *	27.75 *
1977 Twins	8	62	2.4660	-0.0043 ± 0.0010	-4.247 *	-0.480 *		
1976 Fawns:								
Twins	6	36	2.6132	-0.0162 ± 0.0021	-7.715 *	-0.798 *	0.01	2.68
Twins Raised As Singles	2	14	2.3698	-0.0095 ± 0.0033	-2.917 *	-0.644 *		
Males	4	25	2.5943	-0.0151 ± 0.0028	-5.417 *	-0.748 *	0.34	0.09
Females	4	25	2.5063	-0.0140 ± 0.0023	-6.016 *	-0.781 *		
Of Primiparous Dams	2	8	2.7991	-0.0242 ± 0.0032	-7.464 *	-0.950 *	1.67	11.60 *
Of Pluriparous Dams	6	42	2.4603	-0.0113 ± 0.0018	-6.192 *	-0.699 *		
By Birth Weight Classes								
2.00 - 2.49 kg	4	25	2.5319	-0.0147 ± 0.0026	-5.587 *	-0.758 *		
2.50 - 2.99 kg	3	18	2.6273	-0.0161 ± 0.0030	-5.295 *	-0.797 *	0.15	0.70
3.00 - 3.49 kg	1	7	2.3902	-0.0090 ± 0.0044	-2.051	-0.676		
1977 Fawns:								
Twins	8	62	2.4660	-0.0043 ± 0.0010	-4.247 *	-0.480 *	4.00	1.92
Singles	1	4	2.6149	-0.0137 ± 0.0085	-1.604	-0.750		
Males	6	48	2.4781	-0.0044 ± 0.0012	-3.715 *	-0.480 *	1.04	0.27
Females	3	18	2.4540	-0.0060 ± 0.0022	-2.638 *	-0.550 *		
Of Primiparous Dams	2	16	2.6290	-0.0079 ± 0.0023	-3.435 *	-0.676 *	0.06	4.30
Of Pluriparous Dams	7	50	2.3980	-0.0032 ± 0.0011	-2.888 *	-0.384 *		
By Birth Weight Classes								
2.00 - 2.49 kg	2	16	2.4779	-0.0045 ± 0.0023	-1.945	-0.461		
2.50 - 2.99 kg	4	30	2.5005	-0.0056 ± 0.0015	-3.619 *	-0.564 *	0.03	0.52
3.00 - 3.49 kg	3	20	2.3778	-0.0030 ± 0.0018	-1.640	-0.360		

¹Number of Individual Fawns

²Number of Observations

³F-test comparing intercepts of regression

⁴F-test comparing slopes of regression

* Significant, $P \leq 0.05$

Within the 1977 sample no significant differences were found between the regression equations for any of the fawn groups.

With the exception of the 1 high birth-weight fawn in 1976 (n=7), the 1 single fawn in 1977 (n=4), the 2 low birth-weight fawns in 1977 (n=16), and the 3 high birth-weight fawns in 1977 (n=20), all linear regression equations of $\ln NB$ exhibited significant negative correlations with increasing fawn age and significant negative slopes not equal to zero.

5. Total number of suckling bouts/fawn/24 hours with one or more successful suckling attempts, NSB.

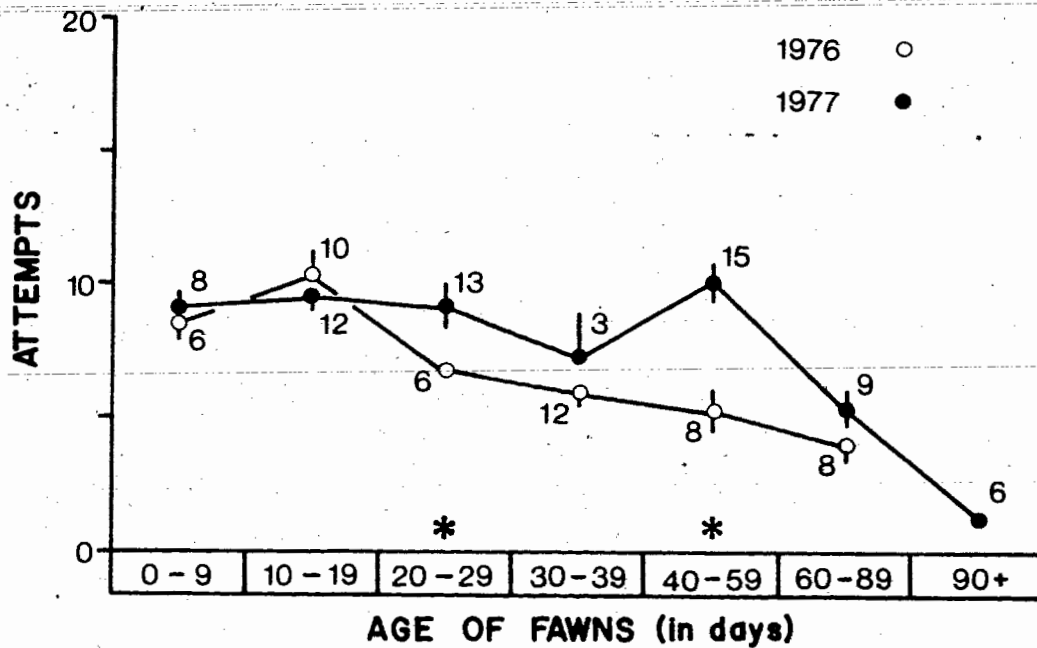
The decline in NSB by age groups was not apparent until after 60 days in 1977 fawns (Kruskal-Wallis rank test, $H_C = 21.48$; 5 df) and until after 20 days in 1976 fawns ($H_C = 8.73$; 2 df). The 1977 fawns exhibited significantly greater NSB than 1976 fawns only in the 20-29 and 40-59 day age groups (Figure 7). The gradual decline in NSB as age increased was most noticeable in the age specific data for individual fawns rather than in the age group specific data.

Between year comparisons of regression equations of $\ln (NSB + 1)$ regressed against age showed that the all-fawn

Figure 7. Changes in the mean number of suckling bouts/fawn/24 h with one or more successful suckling attempts with increasing age ($\bar{x} \pm$ S.E.).

Legend as for Figure 3.

NUMBER OF SUCKLING BOUTS / FAWN / 24 h
WITH ONE OR MORE SUCCESSFUL SUCKLING



and all-twin fawn groups in 1977 had significantly greater intercept values than these fawn groups had in 1976, although no differences in the slope values were found (Table 8). Because of the significant differences between regression equations for each sample year, all subsequent analyses were carried out on within year samples only.

Within the 1976 sample no statistical differences were found between regression equations for either twin and single fawns or for male and female fawns. However, the two fawns of primiparous dams exhibited significantly higher intercepts and steeper slopes compared to fawns of pluriparous dams. Fawns born in the 2.50-2.99 kg birth-weight class were also found to have significantly higher intercepts and non-significantly different slopes than the fawns born within either of the other 2 birth-weight classes.

Within the 1977 sample, the only significant differences found between regression equations occurred where the twin fawns exhibited significantly greater intercepts and non-significantly different slopes than the single fawn.

With the exception of the 1 fawn in the 1976 sample of high birth weight ($n=7$), all linear regression equations of $\ln(\text{NSB} + 1)$ exhibited significant negative correlations with increasing fawn age and significant negative slopes not

Table 8. Summary of test statistics derived from between group comparisons of simple linear regression equations of ln (number of suckling bouts + 1 per fawn per 24 hours, with one or more successful suckling attempts) on age. Statistical significance measured at $P \leq 0.05$. Regression equations in the form $\ln(Y + 1) = a + bX$. -Back transformed regressions may be calculated in the form $Y = \exp(a + bX) - 1$.

	N^1	n^2	a	b \pm S.E. _b	t_b	r	F_a^3	F_b^4
1976 Fawns	8	50	2.3949	-0.0110 \pm 0.0017	-6.360 *	-0.676 *	10.49 *	0.01
1977 Fawns	9	66	2.6047	-0.0113 \pm 0.0012	-8.709 *	-0.736 *		
1976 Twins	6	36	2.4062	-0.0119 \pm 0.0020	-5.693 *	-0.698 *	13.72 *	0.08
1977 Twins	8	62	2.6310	-0.0111 \pm 0.0012	-8.867 *	-0.753 *		
1976 Fawns:								
Twins	6	36	2.4062	-0.0119 \pm 0.0020	-5.693 *	-0.698 *	0.62	0.79
Twins Raised As Singles	2	14	2.3521	-0.0083 \pm 0.0031	-2.657 *	-0.608 *		
Males	4	25	2.3955	-0.0109 \pm 0.0026	-4.101 *	-0.649 *	0.01	0.003
Females	4	25	2.3947	-0.0111 \pm 0.0023	-4.767 *	-0.704 *		
Of Primiparous Dams	2	8	2.4394	-0.0181 \pm 0.0028	-6.435 *	-0.934 *	6.95 *	6.93 *
Of Pluriparous Dams	6	42	2.3514	-0.0086 \pm 0.0017	-4.785 *	-0.603 *		
By Birth Weight Classes								
2.00 - 2.49 kg	4	25	2.3519	-0.0108 \pm 0.0025	-4.272 *	-0.665 *	30.42 *	1.54
2.50 - 2.99 kg	3	18	2.4547	-0.0127 \pm 0.0029	-4.255 *	-0.728 *		
3.00 - 3.49 kg	1	7	1.1994	-0.0029 \pm 0.0015	-1.925	-0.652		
1977 Fawns:								
Twins	8	62	2.6310	-0.0111 \pm 0.0012	-8.867 *	-0.753 *	9.95 *	0.13
Singles	1	4	2.2256	-0.0141 \pm 0.0024	-5.698 *	-0.970 *		
Males	6	48	2.6664	-0.0117 \pm 0.0014	-7.927 *	-0.759 *	2.25	0.11
Females	3	18	2.4719	-0.0105 \pm 0.0028	-3.654 *	-0.674 *		
Of Primiparous Dams	2	16	2.6285	-0.0115 \pm 0.0021	-5.492 *	-0.826 *	0.02	0.01
Of Pluriparous Dams	7	50	2.5968	-0.0112 \pm 0.0016	-6.940 *	-0.707 *		
By Birth Weight Classes								
2.00 - 2.49 kg	2	16	2.7201	-0.0145 \pm 0.0032	-4.521 *	-0.770 *		1.29
2.50 - 2.99 kg	4	30	2.5511	-0.0094 \pm 0.0016	-5.755 *	-0.736 *	0.11	
3.00 - 3.49 kg	3	20	2.5726	-0.0107 \pm 0.0024	-4.399 *	-0.719 *		

¹Number of Individual Fawns

³F-test comparing intercepts of regression

* Significant, $P \leq 0.05$

²Number of Observations

⁴F-test comparing slopes of regression

equal to zero.

Initiation and Termination of Suckling Activity

1. Initiation of Suckling Bouts, NB.

During the first 9 days of age no significant differences were found between years in the number of dam or fawn initiated suckling bouts (Table 9). Within year comparisons of the 0-9 day age group showed that the fawns in 1977 initiated a greater NB than their dams. From 10 days of age onwards these fawns persistently initiated greater NB than their dams and greater NB than the 1976 fawns. In 1976 the picture was different as dams only initiated more bouts than fawns from 20-39 days. At other age groups no differences between dams and fawns could be seen. Only on 3 occasions in the 0-9 day age group in 1976 were dams heard to direct vocalizations towards fawns to initiate suckling bouts. I never heard fawns vocalize to initiate bouts, although grunt and whine sounds from both fawns and dams were infrequently heard during bouts.

The 1976 dams commonly stimulated suckling by licking their fawns during the first 59 days. In 1977 dams licked their fawns far less frequently to initiate suckling bouts and, during the first 9 days especially, dam movement acted

Table 9. Change in frequency of suckling bouts (\bar{x} number of bouts/fawn/24h, \pm S.E.) with age of all observed fawns categorized as to initiation behavior (n = number of fawns).

Initiation Type	Age of fawns (days)						
	0 - 9	10 - 19	20 - 29	30 - 39	40 - 59	60 - 89	90 +
1976	6	10	6	12	8	8	
Dam initiated bouts							
Vocalizing	0.50 ± 0.22	0	0	0	0	0	—
Walking	0.50 ± 0.34	2.20 ± 0.63	2.17 ± 0.79	1.67 ± 0.36	0.50 ± 0.19	1.63 ± 0.26	—
Licking	2.83 ± 1.16	3.90 ± 0.72	3.83 ± 1.22	3.08 ± 0.80	2.88 ± 1.16	1.00 ± 0.38	—
Total	3.83 ± 0.98	6.10 ± 0.82	6.00 ± 0.68*	4.75 ± 0.69*	3.37 ± 1.13	2.62 ± 0.18 ¹	—
Fawn initiated bouts							
Teat seeking	7.00 ± 1.61	6.00 ± 1.03	2.50 ± 0.56	3.08 ± 0.47	2.38 ± 0.42	2.00 ± 0.42	—
Tail wagging	0.17 ± 0.17	0	0	0.08 ± 0.08	0	0	—
Total	7.17 ± 1.7	6.00 ± 1.03	2.50 ± 0.56	3.16 ± 0.47	2.38 ± 0.42	2.00 ± 0.42	—
1977	8	12	13	3	15	9	6
Dam initiated bouts							
Walking	2.25 ± 0.41	1.00 ± 0.33	0.77 ± 0.23	0	1.00 ± 0.29	0.33 ± 0.17	0
Licking	1.00 ± 0.46	0.33 ± 0.19	0.54 ± 0.18	0.33 ± 0.33	0	0.11 ± 0.11	0
Total	3.25 ± 0.37	1.33 ± 0.35	1.31 ± 0.31	0.33 ± 0.33	1.00 ± 0.29	0.44 ± 0.18	0
Fawn initiated bouts							
Teat seeking	6.25 ± 0.45	9.83 ± 0.82	8.23 ± 0.57	11.33 ± 0.33	10.00 ± 0.53	7.78 ± 0.55	5.83 ± 0.83
Tail wagging	0.12 ± 0.12	0.17 ± 0.11 ²	0.54 ± 0.31	0.33 ± 0.33	0.60 ± 0.25 ²	0	0
Total	6.37 ± 0.46*	10.00 ± 0.84*	8.77 ± 0.66*	11.66 ± 0.33*	10.60 ± 0.58*	7.78 ± 0.55 ² *	5.83 ± 0.83

* Significantly different between fawns and dams within years, $P \leq 0.05$ (asterisk at higher mean).

1 Dams significantly different between years, $P \leq 0.05$ (placed at higher mean).

2 Fawns significantly different between years, $P \leq 0.05$ (placed at higher mean).

as the most common stimulus. Teat seeking was the most frequently observed behavior employed by fawns in both years to initiate suckling bouts. The tail wagging of a sibling during suckling seemed to stimulate the other sibling to initiate a suckling bout. This was observed more frequently in 1977 than in 1976.

2. Initiation and Termination of Suckling Attempts, NA.

Suckling attempts were classified on the basis of the 4 possible behavioral combinations of initiator and terminator pairs. These were: dam initiated and terminated; fawn initiated and terminated; dam initiated and fawn terminated; and, fawn initiated and dam terminated. Table 10 lists the mean NA of twin fawns by age group for each of these pair types. Statistical analysis of the 1977 data in the 30-39 day age group was not performed due to the small sample size ($n=2$).

The NA initiated and terminated by 1977 dams was significantly greater than that of 1976 dams only during the first 9 days post partum. No differences in NA were found between 1976 and 1977 dams with twin fawns in any age group between 10 and 59 days. Only when fawns were between 60 and 89 days of age were 1976 dams found to initiate

Table 10. Change in frequency of suckling attempts (\bar{x} number of attempts/fawn/24 h, + S.E.) with age of twin fawns only categorized as to initiation and termination behavior (n = number of fawns).

		Age of fawns (days)							
		0 - 9	10 - 19	20 - 29	30 - 39	40 - 59	60 - 89	90 +	
1976	n	4	8	4	8	6	6		
Dam initiated and terminated		1.50 ± 0.28	8.87 ± 2.33	7.50 ± 1.25	5.00 ± 0.80	1.83 ± 0.47	2.50 ± 0.22*	-	
Fawn initiated and terminated		33.50 ± 3.70*	13.00 ± 3.64	3.00 ± 1.91	2.37 ± 1.06	0.66 ± 0.66	0.66 ± 0.42	-	
Dam initiated and fawn terminated		3.75 ± 1.25	5.75 ± 1.12	4.25 ± 1.31	0	0	0	-	
Fawn initiated and dam terminated		6.75 ± 1.75	9.37 ± 1.25	7.50 ± 3.57	4.12 ± 0.76	2.66 ± 0.42	1.66 ± 0.61	-	
Hc ¹		12.16**	3.33	4.12	17.00**	13.70**	13.82**	-	
1977	n	8	12	12	2	14	8	6	
Dam initiated and terminated		7.62 ± 1.25*	2.83 ± 0.40	2.66 ± 0.77	1.50 ²	1.78 ± 0.42	0.52 ± 0.18	0	
Fawn initiated and terminated		9.00 ± 2.22	16.41 ± 2.84	8.33 ± 1.63	2.00	3.07 ± 1.11	1.50 ± 0.62	0	
Dam initiated and fawn terminated		1.37 ± 0.59	0.83 ± 0.32	1.00 ± 0.49	0	0.14 ± 0.09	0	0	
Fawn initiated and dam terminated		39.87 ± 5.42*	35.00 ± 7.44*	20.91 ± 3.61*	75.50	28.35 ± 5.68*	11.00 ± 1.14*	8.33 ± 2.01	
Hc ¹		22.21**	39.15**	31.65**		39.21**	23.15**	22.41**	

* Initiation and termination behaviors within each age group significantly different between years, $P \leq 0.05$ (asterisk at higher mean).

** Initiation and termination behaviors within each age group significantly different within each year, $P \leq 0.05$.

¹ Kruskal-Wallis rank test statistic, corrected for tied ranks.

² Analyses not performed on the 30-39 day age group in 1977 due to the small sample size.

and terminate significantly greater NA than 1977 dams. In 1976 the fawn initiated and terminated NA was significantly greater than that in 1977 only during the first 9 days of age. No differences between years were found in any subsequent age groups. No significant differences between years were found in any age grouping when dam initiated and fawn terminated NA were considered. With the exception of the 30-39 age period, the 1977 sample exhibited significantly greater NA initiated by fawns and terminated by dams than the 1976 sample in all age groups.

Within year comparisons of intergroup differences between these 4 initiation and termination pairs by age group (Kruskal-Wallis rank test) revealed that NA in 1977 were significantly different within each age group. The most commonly occurring behavior pairing in 1977 was fawn initiation and dam termination. In 1976 no significant differences in NA between all 4 of the initiator and terminator pairs were found within the 10-19 and 20-29 day age groups, but significant differences were found within all other age groups. The most commonly occurring paired behaviors in 1976 appeared to be fawn initiation and termination from 0-9 days, dam initiation and termination from 30-39 days, fawn initiation and dam termination from 40-59 days and dam initiation and termination from 60 to 89 days.

Fawn Growth, Weight and Suckling Behavior

Although no significant differences in twin fawn birth weights were found between sample years, the twin fawns in 1977 were significantly heavier at 25 days than the twin fawns in 1976 (Table 11). To account for these between year differences in weight, 2 methods were used to express fawn growth from birth to 25 days. Firstly, an analysis of covariance comparison of regression equation slopes of $\ln(\text{body weight, in kg})$ on age was used (Figure 8). This showed that the regression equation for 1977 fawns had a significantly steeper slope ($F_D = 6.1908$; 1, 80 df) than did that of 1976 fawns, which indicated greater weight gains per day during the first 24 days in 1977 fawns than in 1976 fawns. Secondly, no significant differences between years were found for the average instantaneous growth rates of twin fawns to the observation day presented in Table 11 (Mann-Whitney rank test). These conflicting results suggest that one of the two forms of analysis is inappropriate. Since parametric statistics are more robust than non-parametric statistics (Zar, 1974) the covariant analysis of regression equation slopes probably best represents any real differences in fawn growth between years.

No significant differences were found between years for the average daily frequency and duration of suckling behaviors NA,

Table 11. Comparison of body weights, growth rates and average daily suckling behaviors of twin fawns from birth to 25 days.

Year	Fawn	At 25 days			Birth to 25 days				
		Birth weight, kg	Age, days	Weight, kg	Growth rate x10 ⁻³	Average daily suckling behaviour			
						NA ^a	NSA ^b	DSA ^c	NSB ^e
1976	M18B	2.20	25	5.60	37.4	30	23	40.08	11
	M18C	2.50	25	6.25	36.7	28	23	37.98	10
	MEB	2.50	22	4.20	23.6	41	19	34.92	10
	FEC	2.35	22	4.45	29.0	33	20	35.87	9
	\bar{x}	2.39	23.5	5.13	31.7	33.0	21.25	37.21	10.0
	S.E.	0.07	0.87	0.48	2.90	2.86	1.03	1.15	0.41
1977	M15F	3.24	22 (24) ^f	8.00 (8.19) ^g	41.1 ^h	58	44	45.55	9
	M15G	3.18	22 (24)	7.25 (7.46)	37.5	59	42	37.62	10
	M17BA	2.20	26 (21)	6.15 (5.64)	39.5	27	19	26.55	10
	M17BB	2.50	26 (21)	6.54 (5.77)	37.0	31	22	23.63	9
	M21AC	2.63	22 (24)	6.60 (6.84)	41.8	41	30	22.48	8
	M21AD	2.48	22 (24)	5.77 (5.94)	38.4	42	32	20.67	8
	FED	2.70	24 (23)	5.90 (5.70)	32.6	76	48	38.92	10
	FEE	2.90	24 (23)	6.69 (6.60)	34.8	71	49	44.10	9
	\bar{x}	2.73	23.5	6.61 (6.61)	37.8	50.63	35.75	32.44	9.12
	S.E.	0.13	0.63	0.26 (0.40)	1.1	6.41	4.12	3.60	0.29
	U^i	25.5	16.0	29.0*(28.0)*	27.0	25.5	26.5	19.0	24.5

^a Number of suckling attempts/24 h.

^b Number of successful suckling attempts/24 h.

^c Duration of successful suckling attempts/24 h, in minutes.

^d Number of suckling bouts/24 h.

^e Number of suckling bouts/24 h with one or more successful suckling attempts.

^f 1977 fawn ages on the observation date with ages at nearest known weights in parentheses.

^g 1977 fawn weights interpolated to the observation date with weights at nearest known ages in parentheses.

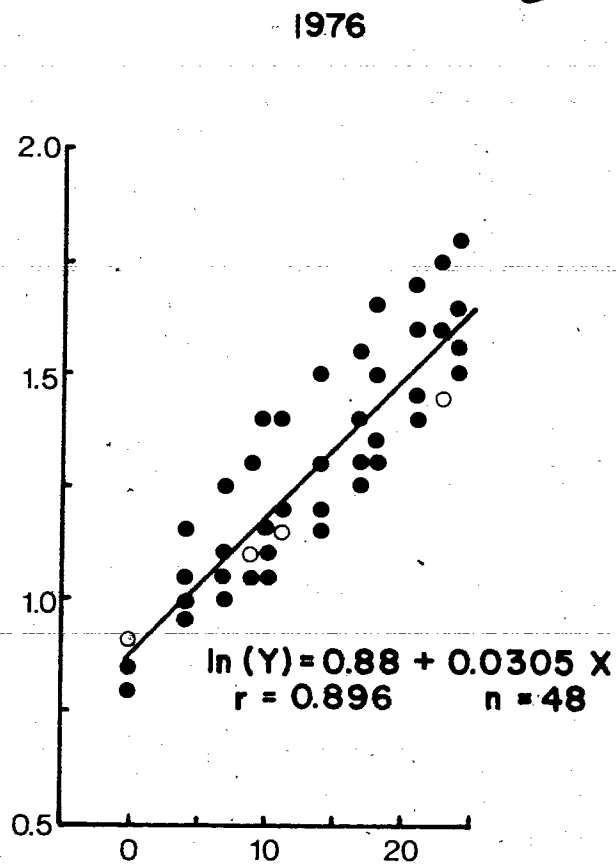
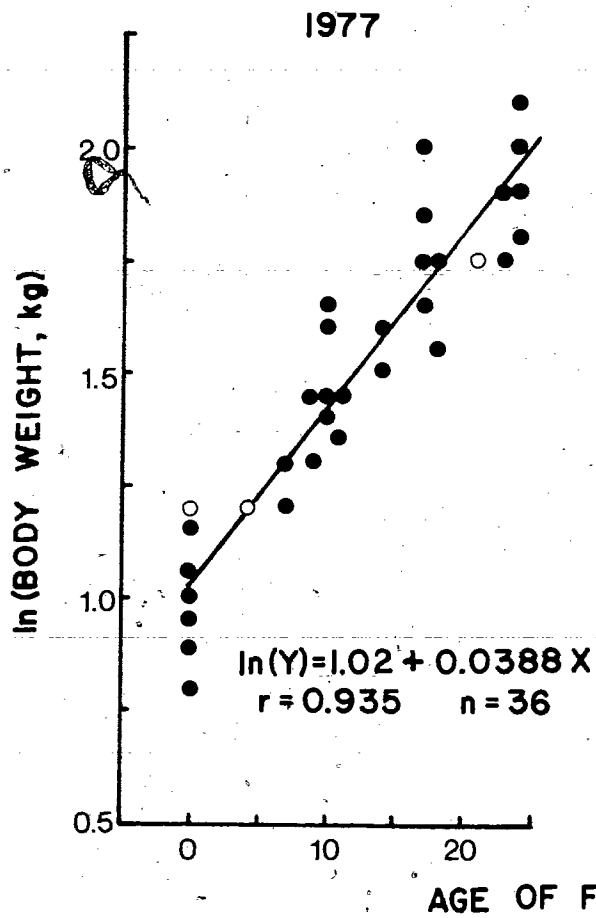
^h 1977 fawn growth rates calculated to the observation date from known ages and interpolated body weights on the observation date.

ⁱ Mann-Whitney rank test statistic comparing means between years.

• $P \leq 0.05$

Figure 8. Regressions of weight on age of twin fawns to 24 days. Regression slopes and correlation coefficients significant to $P \leq 0.05$.

Duplicate weights at age indicated by open circles.

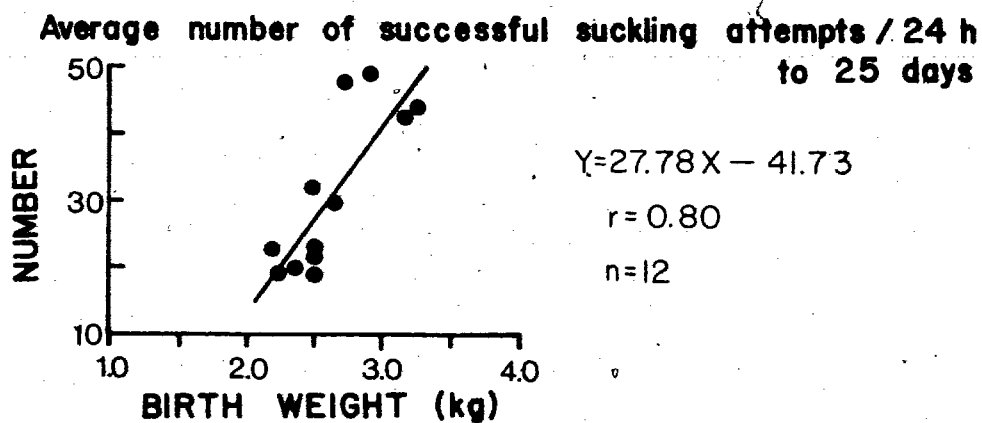
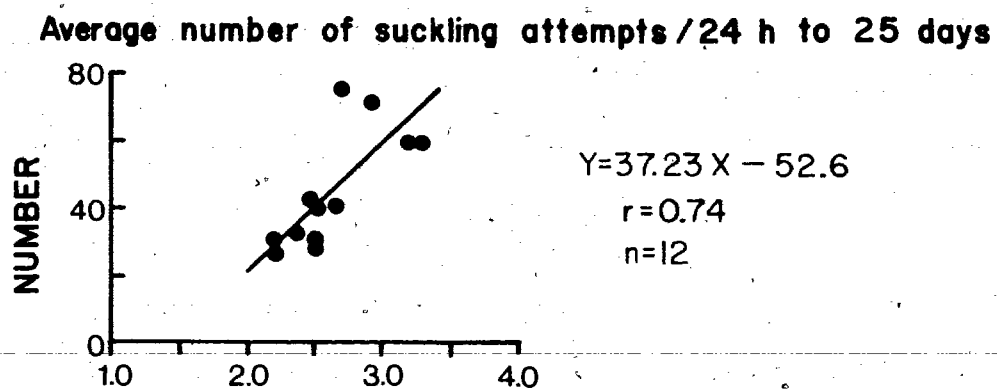
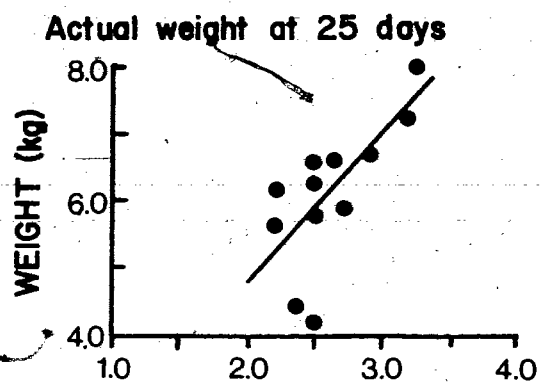


NSA, DSA, NB and NSB during the first 25 days of age (Mann-Whitney rank test, Table 11). Average daily values of these suckling behaviors were not correlated significantly with the instantaneous growth rates to 25 days of age when year samples were pooled. No correlations between fawn birth weight and instantaneous growth rates to 25 days were found in the pooled sample years. However, significant positive correlations in the pooled sample were found when average daily values of NA and NSA behaviors to 25 days and, weight at 25 days were regressed upon birth weight for the 12 twin fawns in Table 11 (Figure 9). These results suggest that heavier-born twin fawns made more suckling attempts per day, were more successful in their suckling attempts per day and gained more weight than lighter-born twin fawns during the first 25 days of age.

Milk Consumption

The milk consumption of 6 twin fawns was measured in 1977 using the mass transfer weighing technique of Sadleir (1980b). Total weights of milk consumed and total suckling durations over 24 h periods were measured for each fawn at 9, 16, 23, 37, 58, 85 and 121 days of age. Measurements taken on 1 of the fawns at 37 days were not analysed due to weighing errors. Daily milk consumption for all measurements were integrated by the method of Sadleir (1980b) to yield estimates of total milk consumption

Figure 9. Regressions of weight at 25 days, average number of suckling attempts/24 h to 25 days and, average number of successful suckling attempts/24 h to 25 days on birth weights of twin fawns in both years. Regression coefficients significant at $P \leq 0.05$.



per fawn to 25 and 60 days of age (actual mean age \pm S.E. = 23.33 \pm 0.84 days and 58.0 \pm 0.63 days, respectively).

Significant positive correlations were found when total milk consumption from birth to both 25 days and 60 days were regressed upon fawn birth weights (Figure 10). Heavier-born fawns were found to consume more milk than lighter-born fawns from birth to these ages. However, no significant correlations were found when total milk consumption was regressed upon absolute weight change during either the 0-25 day or 0-60 day age periods (Table 12). Similarly, no correlations were found when instantaneous growth rates were regressed upon total milk consumption from birth to both 25 and 60 days.

The relationship between absolute 24 h milk consumptions and absolute 24 h suckling durations for each fawn, at each age where milk consumption was measured, is shown in Figure 11. No significant correlation was found when milk consumption was regressed against suckling duration over all 24 h periods of measurement. During the first 4 months, 24 h suckling duration continuously declined. Noticeable declines in milk consumption were not readily apparent until 85 days of age.

The quantity of milk consumed ($\bar{x} \pm$ S.E.) declined from 578 \pm 59 g at 9 days to 271 \pm 85 g at 85 days of age, and the rate of milk intake while suckling, or suckling efficiency, increased sevenfold from 0.43 \pm 0.08 g/s to 3.08 \pm 1.06 g/s ($\bar{x} \pm$ S.E.) over the same age interval (Figure 12). At 4 months, fawns

Figure 10. Estimated total milk consumption of 6 twin fawns from birth to 25 days of age and of those same fawns from birth to 60 days of age regressed on birth weight.

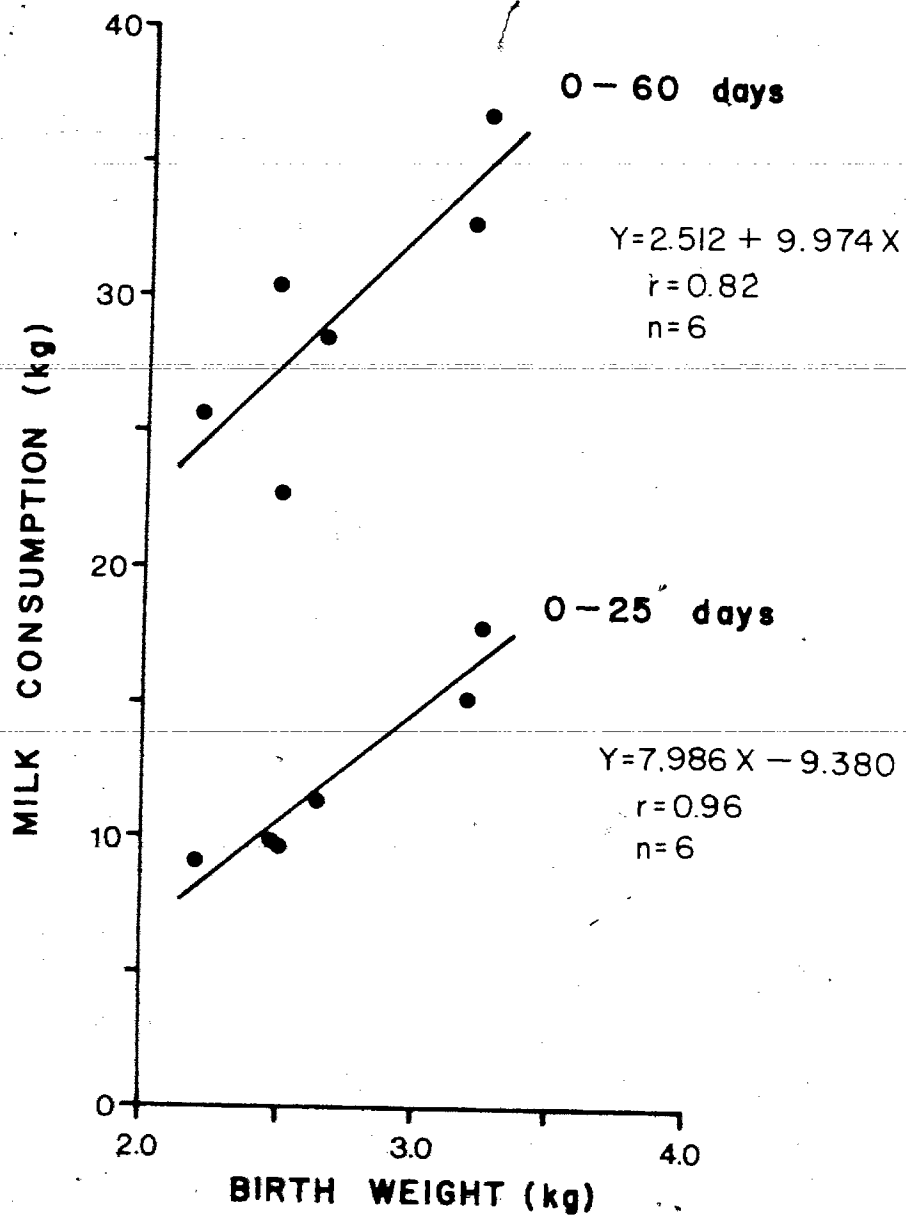


Table 12. Changes in body weight, growth rate, and estimated total milk consumption for 1977 twin fawns from birth to both 25 and 60 days of age.

Fawn	Δ Body Weight (kg)		Estimated Total Milk Intake (g)		Growth Rate $\times 10^{-3}$	
	0 - 25 days	0 - 60 days	0 - 25 days	0 - 60 days	0 - 25 days	0 - 60 days
M15F	4.76	10.17	17791	36798	41.1	40.7
M15G	4.07	7.95	15086	32740	37.5	36.4
M17BA	3.95	9.43	9216	25657	39.5	41.6
M17BB	4.04	9.30	9831	22711	37.0	41.3
M21AC	3.97	9.24	11422	28596	41.8	39.0
M21AD	3.29	9.71	9987	30453	38.4	39.9

Figure 11. Relationship between absolute milk consumption and absolute suckling duration for twin fawns at various ages.

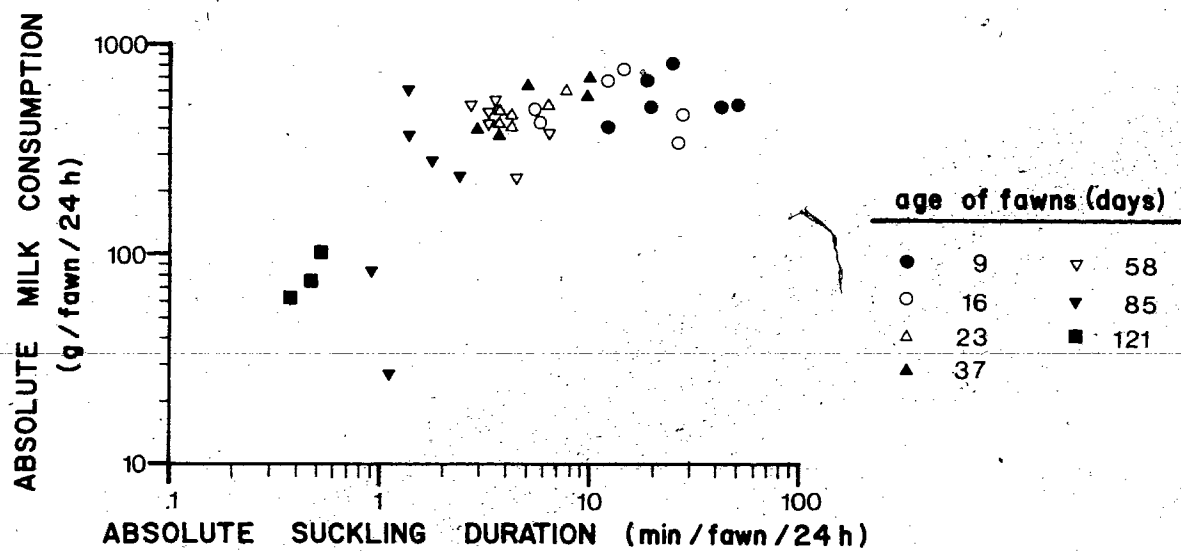
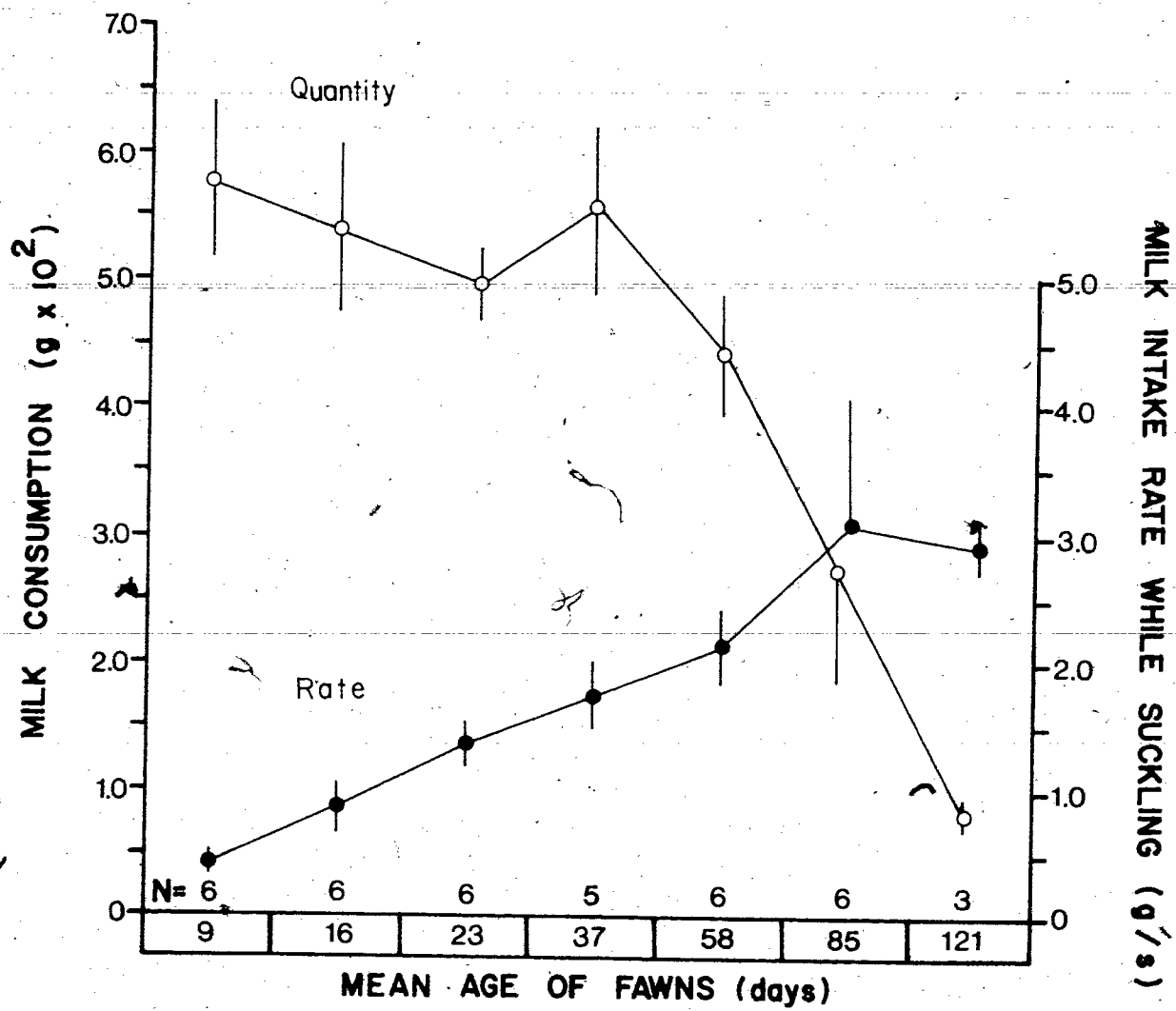


Figure 12. Mean 24 h milk consumption and mean suckling efficiency (milk intake rate while suckling) of twin fawns during 24 h periods with increasing age ($\bar{x} \pm \text{S.E.}$).



continued to consume milk in very small amounts. Of the three fawns which were suckling at this age, consumptive efficiency remained high and each fawn received less than 100 g of milk/24 h. Significant correlations between actual milk consumption and fawn age were not apparent until 85 days of age. At this age the regression equation was $Y=625.47 - 3.73X$; $r=-0.553$; $n=35$ ($P \leq 0.001$). No significant correlations were found when actual milk consumption was regressed upon actual suckling duration for all fawns within each 24 h period at each age. Similarly, regression equations of individual fawns lacked significant correlations between milk intake and suckling duration at each age. No significant correlations were found between milk consumption and suckling durations for all fawns during any one suckling bout at any given age. For example, Table 13 lists the actual values for suckling duration, milk consumption and rates of milk intake for all fawns at 16 days of age.

Up to 25 days of age, when fawns were receiving all their nourishment from milk, no significant differences between siblings were found during any 24 h period for either milk consumption, suckling duration or rate of milk intake (Mann-Whitney rank test). This pattern was also maintained between siblings at 37 and 58 days when fawns were on both a milk and solid food diet. By 85 days the number of suckling bouts in 24 h was too infrequent for statistical analysis between siblings and, at 121 days only one member of each

Table 13. Actual values for suckling duration, milk consumption and rates of milk intake while suckling in 6 bouts over 24 h for twin fawns at 16 days of age.

FAWN

Bout	s ¹	M21AC		M21AD			M17BA			M17BB			M15F			M15G			r ⁴
		g ²	g/s ³	s	g	g/s	s	g	g/s	s	g	g/s	s	g	g/s	s	g	g/s	
1	72	46.2	0.64	69	75.2	1.09	671	152	0.23	565	95	0.17	81	117	1.44	60	57	0.95	0.707
2	0	0	0	0	0	0	509	51	0.10	587	119.8	0.20	30	22.6	0.75	0	0	0	0.808
3	46	144.6	3.14	62	97.8	1.58	90	21.2	0.24	61	31.6	0.52	88	111.6	1.27	0	0	0	0.461
4	57	58.4	1.02	80	112.5	1.41	0	0	0	0	0	0	176	268.6	1.53	277	300.8	1.09	0.948
5	101	124	1.23	136	156	1.15	256	124.2	0.49	286	161.8	0.57	297	160.4	0.54	153	214	1.40	0.831
6	50	124	2.48	0	0	0	0	0	0	140	69.25	0.49	169	101.65	0.60	246	107.8	0.44	0.235
Total	326	497.2	1.53	347	441.5	1.27	1526	348.4	0.23	1639	477.45	0.29	841	781.85	0.93	736	679.6	0.92	0.272
U ⁵	15.0	11.0	10.0				11.0	11.0	13.5				14.0	14.0	14.0				
r ⁶		0.098			0.921			0.605			0.533			0.583			0.653		

- 1 Suckling duration of fawn while suckling dam during a suckling bout, in seconds.
- 2 Absolute milk consumption of fawn while suckling dam during suckling bouts, in grams.
- 3 Absolute rate of milk intake of fawn while suckling dam during suckling bout, in grams/second.
- 4 Correlation coefficient of regression of absolute milk consumption on absolute suckling duration for all fawns within bouts. All insignificant at $P \leq 0.05$.
- 5 Mann-Whitney rank test statistic comparing siblings over 24 hours. All insignificant at $P \leq 0.05$.
- 6 Correlation coefficient of regression of absolute milk consumption on absolute suckling duration for each fawn per 24 hours. All insignificant at $P \leq 0.05$.



IV. DISCUSSION

This investigation was designed to describe the suckling activities of captive, dam-raised black-tailed deer fawns over 24 h periods from birth to 4 months of age. The study identified, described and quantified 5 fawn suckling behaviors (NA, NSA, DSA, NB and NSB) as fawns increased in age. All 5 behaviors were found to decline in either frequency or duration as fawns grew older. The average rates of these declines were described for fawns in each year sample by the slope values of linear equations when lognormal transformations of suckling behaviors were regressed upon known fawn ages. With few exceptions these regression equations demonstrated significantly negative slope and correlation coefficient values. It was also found that fawn suckling attempts throughout the day could be organized into discrete periods of suckling activity and that these periods could be described as suckling bouts. No consistent patterns of suckling bout initiation by either dams or fawns were discernable in each of the 2 years. Fawns were found to initiate suckling bouts most frequently by approaching their dams in a manner described as "teat seeking". Dams were found to employ vocal, licking and movement stimuli when

initiating fawn suckling bouts. When only individual suckling attempts were considered with regard to both the initiator and terminator of each event, variability between years was found. In 1977 the most common pattern was for fawns to initiate suckling attempts and for dams to terminate them at all age intervals. In 1976 this combination of initiation and termination was found most common only between 40 and 59 days of age. During the first 25 days of age, when fawns were on a diet consisting primarily of milk, the suckling behaviors, milk consumption and weight at 25 days of age appeared closely associated with fawn birth weight. Results of linear regression of these variables on birth weight suggested that heavier-born twin fawns make more suckling attempts, are more successful in their attempts to suckle, consume more milk and weigh more at 25 days than lighter-born twin fawns. Significant correlations between actual milk consumption/24 h and fawn age were not apparent until 85 days of age. A lack of correlation between actual milk consumption/24 h and actual suckling duration/24 h was found and was explained by a corresponding increase in the rate of milk intake while suckling, or suckling efficiency, as fawn age increased. Siblings were not found to differ significantly in either their milk consumption, suckling duration or rate of milk intake during any comparable 24 h periods up to 58 days of age. At 4 months of age those fawns which were still suckling were found to consume less than 100 g

milk/24 h on average compared to just under 600 g milk/24 h at 9 days.

Limitations of the Data

Certain limitations in the data, due mainly to the methods of data collection used, should be recognized as influencing the results. The frequency of NSA and NSB, for example, may not be truly representative, as the actual numbers of successful suckling attempts were not recorded on the basis of actual milk transfer from the dam to the fawn. Only suckling attempts which exhibited certain behavioral characteristics, as described and referred to previously in the methods section, were recorded as being successful. Similarly, since milk flow from the dam to the fawn was not measured during the continuous 24 h behavioral observations from which DSA values were derived, the values for DSA presented here are only representative of the time fawns spent with their mouths on their dam's teats. Manual timing of DSA using stop watches may have resulted in over-estimates of time spent on the teats if the reaction and manipulation times of the observers were slow. Since data were collected from captive, rather than from free-ranging deer, the close proximity

of dams and fawns may have increased fawn accessibility to their milk supply. In the wild, lactating does return periodically throughout the day to nurse their young and the fawns respond to the approaching movements of their dams by attempting to suckle (Linsdale and Tomich, 1953; White et al., 1972; Faatz, 1976). As noted in the present study, the movements of dams within the holding pens resulted in the initiation of a considerable number of suckling bouts possibly mediated by the close proximity of mother and young. Under such conditions, dams would not be free to avoid continuous suckling attempts by their fawns. Also, it is not known what effect the presence of either nocturnal lighting or jute sacking on the pen walls (1977 only) had upon the suckling and nursing activities of the fawns and dams, respectively. For these reasons, I suggest that my data represent over-estimates of the suckling activities of free-ranging black-tailed deer fawns.

The higher frequency of behavioral events that were recorded in 1977 than in 1976 may have been caused by the presence of more observers in 1977. The few observers in 1976 may have been less efficient in recording observations due to observer fatigue than the many observers in 1977. However, no differences between years were found in the frequency or duration of behaviors when fawns were less than 20 days old, a period when suckling activity is maximal. The close proximity of the observers to the animals further assured that few behavioral

events were missed in either year. All observers were thoroughly trained in both years. Pre-training of observers tends to reduce over-estimates caused by observer bias and tends to maintain a low, yet constant, bias error attributed to each observer (Norton-Griffiths, 1978). In the present study it was assumed that trained observers maintained a consistently low bias error but this was not tested as it was considered unlikely. As a result, the data was not corrected to account for observer bias prior to data analysis.

Increased suckling activity due to disturbances has been reported in other cervids (Espmark, 1971; Lent, 1974; Faatz, 1976). Sudden disturbances caused by observers occurred infrequently in this study and did cause some fawns to initiate or terminate suckling attempts. Because fawns were accustomed to being handled and to the presence of humans it is doubtful that infrequent disturbances by observers can account for either the wide ranges of individual variation or the annual differences found in suckling behaviors.

Certain methods used in the data analyses may also misrepresent the actual changes in suckling behavior which occurred as fawns grew older. Espmark (1969; 1971) averaged comparable suckling behaviors over 10 day age intervals for both roe deer (Capreolus capreolus) and caribou (Rangifer tarandus). I did this in the present study for comparative purposes. There were some difficulties in comparing data when behavioral

measurements were averaged over 10-day intervals. The age interval averages do not truly represent average behaviors over the 10-day period since fawns were neither observed for the full 10 days nor were fawn ages equally distributed throughout the age interval. Since fawn suckling behaviors decline significantly with age (Tables 4 through 8), observations on fawns whose ages fell within the later part of the age interval would tend to under-estimate suckling behavior compared to fawns whose ages were at the lower end of the interval especially when the age interval is quite wide.

For these reasons the behavioral data were regressed upon known fawn ages and equations derived from these regressions were used for between year and within year comparisons of suckling behaviors. These regression equations also serve to predict a measure of each type of fawn suckling behavior (Y) at any age (X) when the equations are back transformed. However, this technique, as used in this study, also has its limitations. The between year comparisons may have been misrepresented since the data in 1977 were collected over a longer period (121 days) compared to 1976 (81 days). This may have been the cause of significantly different regression equation slope values in each year. This discrepancy could possibly have been overcome in the analyses by dropping data for 1977 fawns after 90 days. For each suckling behavior presented in Tables 4 through 8, the regression equation slopes measure the rate of decline and the

y-intercept values estimate behavior on the date of birth. The latter is not a meaningful estimate of behavior on the birth date since observations did not take place until fawns were at least 3 days old, but is necessary, however, for comparisons of regression equations.

Comparative Behavioral Observations over 24 hours

The declines in suckling behaviors with increasing age of black-tailed deer fawns resemble those described in mule deer (Linsdale and Tomich, 1953), white-tailed deer (Faatz, 1976) and those of other ungulate species (Tyler, 1972; Horejsi, 1972; Shackleton, 1973; Lent, 1974; Stringham, 1974; Kelly and Drew, 1976; Yahner, 1978; Berger, 1979; Podbielancik-Norman et al., unpublished manuscript, 1980). However, in most of the above papers comparable data was not collected over 24 h periods and usually only 1 or 2 young cervids were observed. Quantification of behavioral frequencies and durations of suckling during 24 h periods ensures that the data is a precise measure of daily activity free of the variation which may exist between nocturnal and diurnal suckling activity patterns. For instance, considerable variation in the numbers of suckling attempts of

6-week-old domestic sheep (O. aries) have been reported by various researchers using various length periods of observation: Sojetado (1952) observed 20/24 h; Munro (1955) found 12/16h; and Ewbank (1964) reported 6/12 h. Precise data is also necessary to formulate mathematical equations which both describe and predict the behaviors of the average fawn as it grows older (see Podbielancik-Norman et al., unpublished manuscript, 1980, and, Tables 4 through 8, this study) or when comparing daily behavioral changes to daily changes in milk consumption and growth as in the present study.

The 24 h frequencies and durations of various suckling behaviors of the 17 black-tailed deer fawns in this study are compared with those from 2 roe deer fawns (Espmark, 1969), 3 white-tailed deer fawns (Faatz, 1976) and 7 elk (Cervus canadensis) calves (Podbielancik-Norman et al., unpublished manuscript, 1980) in Table 14. Such a comparison has many shortcomings. Each of these studies were undertaken on captive animals which may have resulted in greater suckling frequencies and durations than in the wild due to the close proximity of the young to their dams. This is suggested with respect to roe deer (Espmark, 1969), elk (Podbielancik-Norman, et al., unpublished manuscript, 1980) and black-tailed deer in my study. There is also considerable variation in the types of behavior reported by these researchers. In the present study I recorded all of the suckling attempts made by fawns, both successful and

Table 14. Comparisons of the mean frequencies and durations of suckling behaviors/young/24h exhibited by black-tailed deer, white-tailed deer, roe deer and elk young with increasing age from birth.

	Age of young, in days						
	0 - 9	10 - 19	20 - 29	30 - 39	40 - 59	60 - 89	90+
<u>NA¹</u>							
black-tailed deer ²	35,55(6,9)	32,55(15,15)	20,33(23,25)	13,59(34,37)	6,32(52,49)	5,12(79,82)	
roe deer ³	33	18	9.8	8.4	4.2		
<u>NSA⁴</u>							
blacktailed deer ²	23-41	21-33	11-21	8-18	6-17	4-6	
roe deer ³	33	9	7.3	7	1.8		
elk ⁵	9.23(0-7)	5.21(8-77)					
<u>DSA⁶</u>							
black-tailed deer ²	35.55-36.97	31.14-32.82	14.05-20.60	8.85-10.78	4.09-11.37		
roe deer ³	68	17.4	11.9	6.3	1.2		
elk ⁷	20.75(5)	13.43(15)	10.03(25)	7.79(35)	5.52(50)		
<u>NSB⁸</u>							
black-tailed deer ²	8-9	10-9	7-9	6-7	5-10	4-5	1.33(120)
roe deer ³	6	6	7	7	3		
white-tailed deer ⁹	6						

¹Number of suckling attempts/young/24 h.

²Means from both years of the present study, with average fawn ages in brackets and 1976 values first and 1977 values second.

³Means calculated from Espmark(1969), his Figures 4, 5 and 6.

⁴Number of successful suckling attempts/young/24 h.

⁵Means given by Podbielancik-Norman et al. (unpublished manuscript, 1980), with ages in brackets.

⁶Duration of successful suckling attempts/young/24 h, in min.

⁷Means calculated from Podbielancik-Norman et al. (unpublished manuscript, 1980), using the equation in their Figure 2 for the ages in brackets.

⁸Number of suckling bouts/young/24 h, with one or more successful suckling attempts.

⁹Mean given by Faatz(1976) for all fawns during the first 120 days post partum.

unsuccessful, and used various behavioral criteria for determining suckling success. Espmark (1969) defined a successful attempt as being any attempt in which the fawn was allowed to suckle for any duration whereas Podbielancik-Norman et al. (unpublished manuscript, 1980) identified a successful attempt whenever the calf was in contact with the teat for greater than a 10 s duration. Faatz (1976) provided no criteria upon which these distinctions were made. Similarly, different systems have been used to allocate suckling attempts into suckling bouts. Faatz (1976) could not differentiate suckling attempts into bouts in white-tailed deer due to the high frequency of suckling attempts which occurred when fawns were under 30 days old. Podbielancik-Norman et al. (unpublished manuscript, 1980) defined each successful suckling as a suckling bout while Espmark (1969) describes suckling activity relative to periods of maternal care which included successful suckling. In the present study I was able to classify a series of individual suckling attempts into a suckling bout on the criterion that bouts were separated by a 0.5 h period during which no suckling attempts occurred (Figure 1). It was possible to classify each bout as being either successful or unsuccessful on the basis of the success of suckling attempts within a bout. My interpretation of Espmark's (1969) care periods is that they are analogous to NSB in the present study, while comparative NA, NSA and DSA were calculated from his data by multiplying the

behavioral frequencies and durations per care period by the number of care periods /24 h. In the comparable reports the above authors only considered suckling bouts which were successful whereas black-tailed deer were seen to involve themselves in some suckling bouts which were not behaviorally successful.

Comparative Aspects of Suckling Frequency

Black-tailed deer fawns appear to attempt suckling more frequently/24 h at each age and, decline in their NA more slowly than do roe deer fawns (Table 14). In both species suckling attempt frequencies were highest when fawns were youngest but the frequency of attempts at later ages did not fall consistently below 25 percent of these earlier values until black-tailed deer fawns were over 60 days of age compared to over 40 days of age for roe deer fawns. These differences may be due to the different holding conditions of the 2 studies as roe deer fawns were held in larger compounds with an abundance of natural vegetation (Espmark, 1969) compared to much smaller pens and pelleted rations in the present study. Roe deer fawns begin grazing after the first week (Espmark, 1969) compared to black-tailed deer fawns which begin nibbling on solid food during the first week (personal observations) but do not begin to consume appreciable amounts until after 25 days (Sadleir,

1980b). Unless solid food intake is measured it is impossible to determine when it begins (Sadleir, personal communication, 1981).

The closer proximity of fawns to their dams in the present study may also account for greater suckling attempt frequencies when compared to roe deer as either the dam's movements and body outline (Stringham, 1974), the sight and sounds of other young suckling (Townsend and Bailey, 1975; Langenau and Lerg, 1976; Kelly and Drew, 1976) or disturbances (Barnicoat et al., 1949; Espmark, 1971) may provide sensory cues which induce fawns to suckle to satisfy either nutritional or non-nutritional emotional needs (Adler et al., 1958).

Higher suckling frequencies may also be related to a lack of licking behavior exhibited by dams towards their fawns. Licking of the young serves as an important olfactory cue in bond formation between ungulate mothers and young (Collias, 1956; Fraser, 1976) and in the maternal identification of young deer (Faatz, 1976). It has been reported that a lack of maternal licking and grooming of white-tailed deer fawns results in a lack of nursing behavior by dams and results in fawn death during the first 72 h post partum (Langenau and Lerg, 1976). Faatz (1976) reports that up to 50 days of age, longer suckling durations occur when dams are licking their fawns than if they are not. In the present study dams licked their fawns very infrequently to initiate suckling bouts, especially in 1977

(Table 9). In this year, fawns initiated suckling bouts more frequently than their dams and more frequently than fawns in 1976 who received more maternal licking. The 1977 fawns initiated more suckling attempts (Table 10) but did not suckle for longer durations (Figure 5) on average than 1976 fawns. Whether a causal relationship exists between the lack of maternal licking and an increase in the frequencies and durations of suckling activities initiated by fawns through some need for maternal care of this sort is uncertain. Such a relationship may be overshadowed by an increase in suckling behaviors due to the close proximity of mother and young under penned conditions.

Aspects of Suckling Duration

Although few differences were found in the declines in DSA with age between years (Figure 5) considerable variations in DSA were found at various ages when compared with other species (Table 14). Mean suckling durations in black-tailed deer fawns did not decline appreciably until 20 days and a gradual decline continued thereafter throughout lactation. The reduction in suckling durations at 20 days preceded the increased solid food intake noted by Sadleir (1980b) as starting at 25 days. Reductions of DSA after 20 days appears to be compensated for by increases in suckling efficiency (Figure 12) and increased

forage intake (Sadleir, 1980b). Comparisons of DSA of fawns in the present study with those of roe deer and elk (Table 14) show that the reduction in DSA occurred 10 days later than in these species. During the first 10 days of age black-tailed deer exhibited a DSA of nearly one-half that of roe deer fawns (Espmark, 1969) but nearly twice that of elk calves (Podbielancik-Norman et al., unpublished manuscript, 1980). These considerable interspecific variations are possibly due to either differences in dam milk yields, suckling efficiencies of the young, or fawn suckling success resulting from greater or lesser tolerances of dams to allow suckling attempts.

Aspects of Suckling Success

Black-tailed deer fawns are not always successful in their suckling attempts (Table 15) as, at all ages some attempts are discouraged by the dam (Table 10). The proportion of successful sucklings declined in 1976 until fawns were between 20 and 40 days old and then began to increase. The increase did not occur in 1977. This general pattern of suckling success has been seen in both roe deer (Espmark, 1969) and elk (Podbielancik-Norman et al., unpublished manuscript, 1980) although the ages at which the lowest percentage of success is attained are somewhat different. Increased success in suckling after this age appears to be due to reductions in the number of attempts made upon the

Table 15. Comparisons of the numbers of successful suckling attempts as a proportion of all suckling attempts by age interval for black-tailed deer fawns, roe deer fawns and elk calves.

	Age of young in days						
	0 - 9	10 - 19	20 - 29	30 - 39	40 - 59	60 - 89	90+
black-tailed deer ¹							
1976	62	66	56	60	86	87	
1977	73	60	60		54	49	16
roe deer ²	100	50	74	83	42		
elk ³	70(5)	55(15)	45(25)	40(35)	45(50)	70(75)	

¹Fawns from the present study.

²From Espmark (1969), calculated from his Figures 4, 5 and 6.

³From Podbielancik-Norman *et al.* (unpublished manuscript, 1980), interpolated from the curve in their Figure 4 for the calf ages in brackets.

dam relative to the number of attempts allowed by the dam. Similarly, NSB also declines in response to the reductions in both NSA and NB. It has been suggested that dams may allow some suckling attempts to be successful to maintain a continued bond with their fawns (Robbins and Moen, 1975; Faatz, 1976; Sadleir, 1980b).

Milk Consumption and Suckling Behavior

In contrast with the declines in suckling behaviors with age, the absolute 24 h milk consumption in the 1977 fawns did not change significantly during the first 58 days of age and significant declines were not noticeable until 85 days (Figure 12). These findings are in agreement with those of Sadleir (1980b) for fawns of this species where a larger fawn sample was used. Although he found peak daily milk intakes of an average fawn to occur between 1 and 5 weeks, significant declines in the mean milk consumption did not occur until 65 days of age. In contrast, milk consumption of bottle-fed white-tailed deer fawns increased initially and then decreased as fawn weight increased (Robbins and Moen, 1975). A similar pattern of increased milk consumption over the first several weeks was found in both elk calves (Podbielancik-Norman et al., unpublished manuscript, 1980) and red deer (Cervus elaphus) calves (Arman et al., 1974) before declines in consumption were

noted.

As no significant correlations were found between absolute milk consumption/24 h and absolute suckling duration/24 h for 1977 fawns (Figure 11) it appears that suckling duration is not an appropriate measure of milk consumption in black-tailed deer fawns. Geist (1971) suggested that suckling duration in both bighorn sheep and Stone sheep lambs in the wild could be used as an index of milk production by their ewes, and that estimates of population quality could be obtained based upon this assumption. This method was used subsequently by Horejsi (1972), Shackleton (1973) and Berger (1979) to assess qualitative differences between wild bighorn sheep populations. My data suggests that measures of suckling duration cannot be used to indicate milk consumption in black-tailed deer fawns since DSA declines with age during the first 2 months and milk consumption does not. Fawns apparently compensate for lower DSA as they grow older by increasing their efficiency of milk intake while suckling (Figure 12). Increased suckling efficiency may be due to either increased strength of the tongue or increased negative pressures which develop within the buccal cavity as the fawn grows older (Cowie and Tindal, 1971). It has been suggested that increased suckling efficiency in elk calves may also be due to the increased ability of the cow to let-down milk (Podbielancik-Norman et al., unpublished manuscript, 1980) but little is known of this mechanism in either wild or domestic

mammals (Grosvenor and Mena, 1974).

It is doubtful too that either NA, NSA, NB or NSB would serve as an index of milk consumption since these behaviors also decline with increasing age even though NB and NSB exhibit the most gradual temporal declines. Additionally, during any one suckling bout within a 24 h period both milk consumption and suckling duration varies considerably between fawns as each fawn consumes milk at different rates (Table 13). The variability in the rates of milk intake probably reflects either the differing degrees of fawn hunger and satiation, the variability in dam milk production over short time intervals, the variation in milk supply within each quarter of the udder, the responsiveness of the dam to let-down milk or possibly, a combination of all of these factors.

For these reasons, fawn suckling behaviors should not be used as indicators of milk consumption unless measures of absolute suckling behaviors are collected in conjunction with absolute quantities of milk consumed. For instance, during the first 25 days of age, 1977 fawns showed significant positive correlations when average daily milk consumption was calculated from Table 12 using the ages in brackets in Table 11 and regressed upon the average daily suckling behaviors NA, NSA and DSA presented in Table 11. The relationships between these variables are somewhat misleading, however, as both the behavioral and milk consumption values were not only obtained at

different fawn ages but also were estimated by integrations and interpolations to different ages. These estimates were further derived from few data points per fawn and it was assumed that milk consumption and behaviors did not vary from birth to the ages at the first data points.

Aspects of Weaning

Gradual and reciprocal changes in the behavior, anatomy and physiology of both mother and offspring are involved in the weaning process (Lent, 1974). Should either the frequency of suckling and/or the quantity of milk removed from the mammary gland be reduced, milk secretion from within the glandular tissue begins to slow and eventually ceases altogether (Schmidt, 1971; Grosvenor and Mena, 1974). Although the hormonal mechanisms underlying this natural decline in milk secretion are poorly understood, a reduction in milk secretion appears to coincide with a reduction in the nutritional dependency of the young on its maternal milk supply. The gradual transition from milk to solid foods is called weaning (Grosvenor and Mena, 1974).

Behavioral changes in suckling activity which lead to weaning commonly follow a similar pattern in many cervid species (Linsdale and Tomich, 1953; Altmann, 1963; Espmark, 1969, 1971; Stringham, 1974; Lent, 1974; Faatz, 1976; Podbielancik-Norman et

al., unpublished manuscript, 1980). Suckling activity in these species declines with increasing age of the young and there are changes in the behavioural patterns of mother-young interactions as well. During the first 2 weeks post partum the dam initiates most suckling bouts in which the young terminates the majority of all suckling attempts. From 2 weeks to 1 month, suckling bouts and suckling attempts may be initiated and terminated by either the dam or the young. During this period the young may initiate suckling attempts on dams other than their own. Usually, after 1 month of age, suckling bouts are initiated by the young and suckling attempts are terminated by the dam.

In the present study black-tailed deer did not exhibit this generalized pattern of cervid suckling behavior (Tables 9 and 10). Consistently greater numbers of suckling bouts were initiated by fawns than dams and more suckling attempts were terminated by dams than fawns at all ages in 1977. In 1976, dams did not initiate significantly greater numbers of bouts than fawns when their fawns were under 20 days of age but dams terminated greater numbers of suckling attempts than fawns after this age. These deviations from the general pattern of suckling behavior associated with weaning in cervids are possibly due to the captive situation as fawns had continual access to their dams. Quite possibly, behavioral conflicts may have occurred between mother and offspring over the available milk supply as proposed by Trivers (1974).

If weaning in cervids is initiated when dams begin to terminate suckling attempts, as suggested by Lent (1974), then black-tailed deer fawns in this study were being behaviorally weaned when less than 10 days old. Since at this age no appreciable quantities of solid food are consumed (Sadleir, 1980b), the concept of weaning as presented by Lent (1974) obviously cannot be applied to black-tailed deer. Pain inflicted upon dams when fawns either bunt the udder or bite the teats may be an important determinant which triggers dam termination of suckling attempts especially if the suckling frequency is high when in captivity.

I did not observe fawns suckling dams other than their own as individual families were isolated from each other. Cross-suckling of dams has been reported in elk (Podbielancik-Norman et al., unpublished manuscript, 1980), reindeer (Espmark, 1971) and white-tailed deer (Faatz, 1976). However, during casual observations of deer kept in a larger paddock, I noted one fawn successfully suckling a dam while both her own twins were suckling and, in another instance one fawn attempted to suckle an adult buck. Both fawns involved were of unknown age and hence this behavior relative to the weaning sequence is not known. In another study on suckling behaviour (Drinnan and Sadleir, 1981), I observed a young cetacean calf cross-suckling a sub-adult female on numerous occasions at ages under 4 months.

Between the ages of 80 and 120 days, fawn suckling activity was observed infrequently suggesting that by these ages weaning was still in progress but was nearing completion. Behavioral weaning is apparently completed between 3 and 5 months of age in black-tailed deer (Cowan, 1956) and either between 60 and 75 days (Dixon, 1934) or by 5 months (Linsdale and Tomich, 1953; Einarsen, 1956) in mule deer. White-tailed deer dams begin to wean their fawns at 3 months of age (Faatz, 1976) and weaning is usually completed between 5 and 6 months (Severinghaus and Cheatum, 1956).

The length of the lactation period in Odocoileus is variable. Ceasation of milk production in penned black-tailed deer may occur as early as 84 days (Sadleir, 1980a) or extend to 283 days (Mueller and Sadleir, 1977). Mule deer dams in the wild have been observed to nurse their fawns at 9 months and their yearlings and fawns of the year simultaneously (Hanson, 1958). Although suckling behavior was not observed, free ranging white-tailed deer dams frequently have milk in their udders well after the breeding season (Scanlon et al, 1976) and as late as March of the following year (Scanlon and Urbston, 1978).

In my study, milk consumption by 1977 fawns did not significantly decline with age until fawns were between 58 and 85 days old. This result suggests that although behavioral weaning begins during the first week of age when dams begin terminating suckling attempts (Lent, 1974), nutritional weaning,

as determined by reductions in milk consumption, does not begin until after the second month. By 90 days of age, the proportion of milk in the diets of black-tailed deer fawns is 50 percent and declines thereafter as fawns increase in age (Sadleir, 1980b). By 120 days fawn milk consumption was less than 100g/24 h. Maintenance of milk production and suckling behaviors at reduced levels in late lactation may thus be important in maintaining the mother-young bond (Robbins and Moen, 1975; Faatz, 1976; Sadleir, 1980b) rather than providing the fawn with an important source of protein prior to winter (Smith et al, 1975). It has been suggested by Sadleir (1980b) that behavioral weaning in black-tailed deer fawns occurs later than is metabolically necessary to sustain growth since the growth of early weaned fawns does not differ from those of late weaned fawns. Late weaned fawns may receive the benefits of a prolonged social association with their dams at no physiological cost to the dam since milk yields of dams and milk consumption by fawns are considerably reduced after 90 days post partum (Sadleir, 1980b).

Intergroup Comparisons of Suckling Behavior

Between Years

Significant differences in suckling behaviors NA, NSA, DSA, NB, and NSB with increasing fawn age were found between 1976 and 1977 fawns when linear regression equations for both the all-fawn and all-twin fawn groups were compared (Tables 4 through 8). Differences between the equations for each year were noted when either the slope or intercept values or both were found to be significantly different. The regression equation slopes for suckling behaviors NSA, DSA and NSB were not found to be significantly different between years. The similarity of these slope values suggests that for each behavior, the rate of decline with increasing fawn age was similar between years. The 1977 fawns tended to exhibit higher frequencies for each of these behaviors as demonstrated by the higher intercept values of the regression equations. The regression slopes for suckling behaviors NA and NB were significantly steeper in 1976 than in 1977 suggesting that the frequency of these behaviors declined more gradually in 1977 than in 1976. These between year differences in slope values for NA and NB may be artifacts of the analysis since data for 1977 fawns were collected over a

longer period (121 days) as compared to 1976 fawns (81 days). It remains to be seen if these between year differences would have been present if data for 1977 fawns after 90 days of age was excluded from the regression analyses of these behaviors. In other studies of the 24 h suckling behaviors of roe deer (Espmark, 1969) and elk (Podbielancik-Norman et al., unpublished manuscript, 1980), where comparable data were collected over many years, no attempts were made to investigate between year differences in suckling behaviors.

Since between year differences in the suckling behaviors NA, NSA, DSA, NB and NSB were found to exist, similar interpretations of the linear regression equations within each year will next be made for comparative similarities and differences in these behaviors for twin and single fawns, fawns of primiparous and pluriparous dams, male and female fawns and, fawns born in different birth-weight classes. Where statistically significant differences were found between linear regression equations of each of these groupings of fawns in each year, the sample size was always consistently small for one of the fawn groups being compared (Tables 4 through 8). It is therefore questionable whether or not the behavioral differences in suckling between these fawn groups within each year are biologically significant.

Twin and Single Fawns

In white-tailed deer, twin fawns suckle for longer durations/24 h than single fawns during the first 72 h post partum (Langenau and Lerg, 1976) and single fawns suckle more frequently/24 h than twin fawns during the first week (Faatz, 1976). Unfortunately, these authors provide no statistical evidence which support these claims. In domestic sheep, twin lambs suckle more frequently during daylight hours than single lambs (Munro, 1955; Ewbank, 1967). Since nocturnal suckling frequencies were not reported by these authors any real differences in the 24 h suckling behaviors of twin and single lambs remains obscured. In the present study on black-tailed deer, intergroup comparisons of NA in 1976 showed that 6 twins did not suckle any more frequently immediately after birth than 2 singles because the intercept values were not significantly different. However, in this year, twin fawns declined in NA significantly faster than single fawns as demonstrated by the steeper regression slope for twin fawns. Differences in NA between twin and single fawns in 1977 were not apparent although only one fawn was in the single fawn sample. Single and twin fawns in 1976 did not differ in either their NSA, DSA, NB or NSB regression equations. On the other hand, although 1977 twin and single fawns exhibited no differences in NB, twin fawns in this

year consistently exhibited greater NSA, DSA and NSB at the intercept than singles although the rate of declines, as measured by the regression slope values of these behaviors, were similar. The variability between twin and single fawn suckling behaviors in 1977 is almost certainly related to the small sample from 1 single fawn. This fawn was observed on only 4 occasions each after 22 days post partum when behavioral frequencies had already declined below the maximums recorded in younger aged fawns. Even if differences in the frequencies and durations of suckling behaviors do exist between twin and single fawns, the milk yield of dams with twins is twice that of dams with single fawns (Sadleir, 1980a). This suggests that milk consumption by twins and single fawns are equal since Sadleir's (1980a) milk yields were determined by fawn consumption.

Past Reproductive Experience of Dams

Cowan (1974) suggested that the maternal bond between mother and young is more effectively established by dams experienced at raising young (pluriparous) compared to inexperienced dams (primiparous). However, Espmark (1969) reported that in roe deer, primiparous dams initiated care towards their fawns significantly more frequently than

pluriparous dams. In horses, Tyler (1972) found no differences in suckling bout length between foals of dams of different parity. Langenau and Lerg (1976) observed that the time from birth to first nursing, or the time to form a bond between the neonate and the dam, as described by Fraser (1976), was not significantly different between white-tailed deer fawns born to dams of differing parity. In the present study, the parity of the dam had no significant effect on fawn suckling behaviors in 1977. However, fawns of primiparous dams in 1976 reduced their frequency of suckling activity faster than fawns of pluriparous dams as described by the significantly steeper regression equation slopes for all suckling behaviors recorded. In each year, however, only one dam was primiparous and although this trend was exhibited in one year it was not repeated in the next. The sample sizes were insufficient to adequately determine distinct differences between fawns raised by dams of differing reproductive experiences.

Male and Female Fawns

Trivers (1974) has suggested that female mammals may invest parental care differentially between offspring of each sex to further promote the dams own fitness. During periods of

nutritional stress when females are in declining physiological condition, it has been suggested by Trivers and Willard (1973) that females should produce a lower ratio of males to females. Female black-tailed deer on a high plane of nutrition in prime physiological condition appear to select for males in utero as male birth weights are higher than females (Mueller and Sadleir, 1980). Behavioral differences between fawns of either sex may be important determinants of fawn mortality. Jackson et al. (1972) observed that male white-tailed deer fawns are more active and exhibit longer durations of activity compared to female fawns during daylight hours in their first 40 days. These workers suggested that this increased male activity, which consisted primarily of suckling activity, may attract predators and account for the higher male fawn mortality within the species. Older male black-tailed deer fawns show higher mortality than females which may be attributed to their greater activity levels, curiosity and independence compared to females (Taber and Dasmann, 1954). It has been suggested that dams of both white-tailed deer (Robbins and Moen, 1975; Faatz, 1976) and black-tailed deer (Sadleir, 1980b) allow their young to suckle late in lactation primarily to maintain a close bond of association. In the wild, female black-tailed deer fawns appear to be much more closely attached to their dams than male fawns during the first year of life (Dasmann and Taber, 1956).

Comparison of linear regression equations for male and female fawns revealed, with one exception, that no differences in suckling behaviors NA, NSA, DSA, NB and NSB occurred between the sexes. However, in 1977, 3 female fawns exhibited significantly greater intercept values for NA than males but the rates of decline in this behavior were similar. Such differential suckling behavior is most likely due to the activity of 2 female fawns, FED and FEE, and the passive nature of their dam. The dam spent considerable time in a recumbent position and her fawns made repeated attempts to suckle while she was lying down. Unlike other dams in this study she did not often stand to discourage her fawns from suckling in this position and consequently, up to 52 days of age her fawns exhibited consistently higher NA than any other fawns. The ease of access to the dam's udder and the passive response of the dam to such frequent suckling attempts may be more responsible for the sexual differences in NA than the gender of the fawns. Even if NA is greater in either sex, Mueller and Sadleir (1980) found no differences in the growth rates of suckling black-tailed deer fawns when the sexes were compared. In contrast, Fletcher (1971) noted that in domestic sheep the sex of the lamb did not effect the suckling frequency although males grew faster than females.

Fawn Birth Weight

The birth weight of the young may have an effect on suckling behavior, milk consumption and growth. Ewbank (1967) reported that in domestic sheep, suckling frequencies of twin lambs were greater during the first 6 weeks in a group of low birth-weight lambs compared to a high birth-weight group and suggested that suckling frequency may increase due to lower weight gains, lower milk yields and greater hunger in the low birth-weight group. However, within limits, the frequency of lamb access to their ewes effects neither milk consumption (Munro and Inkson, 1957) nor growth rates (Louca, 1972). I found no differences between the regression equations of suckling behaviors on age for fawns in the three birth-weight classes (Tables 4 through 8) with the exception of NSB exhibited by 1976 fawns. This difference is due to the 1 fawn in the over 3.00 kg weight class which exhibited NSB behavior which did not correlate significantly with increasing age.

Grouping fawns into birth-weight classes in this fashion may misrepresent the effects which birth weight has upon fawn suckling behavior. The significant positive correlations found in Figures 9 and 10 suggest that suckling behaviors, milk consumption and weight attained during the first 25 days of age for each fawn are related to the fawn's birth weight. During this period, heavier-born fawns may exhibit greater average

daily NA and NSA suckling behaviors, consume more milk and attain greater body weights than lighter-born fawns due to the greater metabolic requirements of heavier-born fawns. Since metabolic rate in deer is a power function of body weight (Moen, 1973), heavy-born fawns would have greater metabolic rates, higher metabolic requirements and greater energy intakes, as measured by milk consumption, than lighter-born fawns. From my data, it appears that fawn birth weight may serve as an indicator of average daily NA and NSA suckling behaviors, total milk consumption and attained weight during the first 25 days of age. Since this age period is indicative of rapid fawn growth (Cowan and Wood, 1955), high milk yield by dams (Sadleir, 1980a), peak levels of fawn milk intake (Sadleir, 1980b), and high fawn mortality (Cook et al., 1971), heavier-born fawns may have a selective survival advantage over lighter-born fawns by obtaining more milk energy through the exhibition of more frequent NA and NSA suckling behaviors in a birth weight related fashion.

In contrast to the reports of compensatory growth of light birth-weight fawns of this species (Mueller and Sadleir, 1980) the fawns of low birth-weights showed no compensatory growth during the first 25 days when on milk diets (Figure 9). This is probably due to their relatively lower values of NA, NSA, milk consumption and weight gain than heavier-born fawns since fawn growth rates during this period are related to the amounts of

milk consumed (Sadleir, 1980b).

Individual Variation in Suckling Behavior

Considerable individual variation in suckling behaviors existed between fawns in captivity. This wide variation is shown by the low regression coefficients when suckling behaviors were regressed on age (Tables 4 through 8). Some causes of this variation, such as fawn size at birth, maternal behavior, access of fawns to dams under captive conditions, milk consumption, growth, foraging behaviors, disturbances and social facilitation have previously been discussed. Other factors may also account for this variability. Reductions in the quantity of food available to pregnant white-tailed deer has been shown to reduce the degree of maternal care given to newborn fawns during the first 72 h post partum (Langenau and Lerg, 1976). These authors found that poorly fed does in winter had a high rate of maternal rejection of their offspring, as measured by their refusal to nurse, even though milk was present in the udder. However, in my study the nutritional status of the dams did not vary either within or between years as individuals were maintained throughout pregnancy and lactation on high quality feed available ad libitum. It is therefore unlikely that the variation in fawn suckling behaviors, both within and between

years, are entirely due to any nutritional differences between dams.

Prior to 20 days of age fawns in both years displayed similarities in each of their NA, NSA, DSA, NB and NSB suckling behaviors resulting from a wide range of individual variation in suckling activity (Figures 3 through 7). Varying birth weights, metabolic rates and metabolic requirements, as previously mentioned, may be important causes of this individual variation up to 25 days.

After 20 days of age, the variations in fawn suckling behaviors found both within and between years (Figures 3 through 7) may possibly be attributed to declines in dam milk yields coupled with reductions in milk consumption, increases in forage intake and differing rates of rumen development. Arnold et al. (1979) reported that in domestic sheep the milk yield of the ewe is a major determinant in the strength of the ewe-lamb bond, with a threshold level below which behavioral weaning occurs. Milk yields in black-tailed deer show considerable variation between dams which are not related to either the age or weight of dams or to their sequence of lactation (Sadleir, 1980a). Peak milk yields in this species are variable, occur between 10 and 37 days post partum and decline gradually thereafter (Sadleir, 1980a). Since fawns increasingly consume larger though variable proportions of their dietary intake from solid foods after 25 days the proportion of total energy intake from milk declines as

lactation proceeds (Sadleir, 1980b). Fawns thus affected by varying milk yields, milk consumption and solid food intake may similarly vary their rate of rumen development. By 15 days of age white-tailed deer fawns are functional ruminants, by 35 days they are essentially dependent upon ruminant digestive processes and, by 4 months they are nutritionally independent (Short, 1964). The rate of rumen development in white-tailed deer fawns, however, is quite variable, especially during the first month post partum, as reductions in milk consumption relative to the nutriment requirements of the fawn may act as a stimulus to increase not only forage intake but also the rates of rumen fermentation and development (Robbins and Moen, 1975).

It was not possible to show the relationships between the variability in fawn suckling behaviors and the variability found both in dam milk yields and in the milk consumption, forage intake and rate of rumen development of fawns in any way other than in a descriptive sense in the present study. In fact, it was outside the scope of this work. Nonetheless, it is possible that the age-specific variation in suckling behaviors of fawns may be mediated by combinations on all of these parameters. As a result of such variability and uncertainty in isolating specific causes of fawn suckling behaviors much more work is necessary to quantify further the relationships between these variables. In this context the present study serves as a preliminary investigation of the subject and is of value to future

researchers in providing descriptions and quantitative data on
24 h suckling activity in black-tailed deer fawns during the
first 4 months of age.

V. CONCLUSIONS

1. Captive black-tailed deer fawns suckle at all hours of the day and night which necessitates continuous 24 h observations to quantify suckling behaviors precisely.
2. Fawn suckling behaviors decline in frequency and duration with increasing age and average values can be calculated to any age using the linear regression equations provided. Some differences in the frequencies and durations of suckling behaviors between males and females, between twins and singles, and between fawns of primiparous and pluriparous dams, and between fawns in different birth-weight classes were found, but these results were not consistent between years. The significance of such differences are questionable due to the small sample sizes used in the analyses.
3. Suckling duration was not found to be correlated with milk consumption and it is suggested that this and other suckling behaviors provide no insight into milk consumption estimates.
4. Fawns begin behavioral weaning by their dams when under 10 days old whereas nutritional weaning does not begin until after 60 days when milk consumption declines noticeably.
5. Birth weight appears to be an indicator of fawn suckling

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activity, milk consumption and attained weight and hence, possible survival when fawns are consuming only milk. During the first 25 days of age, heavier-born twin fawns were found to make more suckling attempts per day, were more successful at suckling per day, consumed greater total amounts of milk, and attained greater weight than lighter-born twin fawns.

6. Fawns were found to increase their suckling efficiency, as determined by their milk intake rates while suckling, to compensate for fewer successful nursing attempts and shorter durations of suckling as they become older. These reductions in suckling behavior were imposed by the dam who terminated most suckling attempts.
7. Suckling behaviors observed in captivity may be altered from that in the wild as fawns have continual access to their dams. In captivity, fawns initiated more suckling attempts and suckling bouts than dams but dams usually terminated more suckling attempts than fawns. The high frequency of fawn initiation and dam termination of suckling activity may be due to harassment on dams by fawns.
8. Siblings were not found to differ appreciably in their 24 h suckling durations, milk consumptions and suckling efficiencies when consuming milk. Lack of sibling differences may be attributed to the captive situation as suckling may be socially facilitated by visual and auditory cues produced by either the dam or other suckling conspecifics nearby.

9. Suckling behavior of fawns was observed up to 4 months of age. At this age, milk consumption was 100 g/24 h or less and suckling occurred infrequently, lasting for very short durations. Suckling at this age would appear to impose little physiological stress upon the dam since milk consumption is low.

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