THE COMPOSITION AND YIELD OF MILK FROM CAPTIVE RED DEER (*CERVUS ELAPHUS* L.)

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(Received 2nd April 1973)

Summary. The gross anatomy of the mammary gland of the red deer is described. A total of 102 milk samples was obtained from six deer (four during a complete lactation). These contained an average of 21.1% total solids (8.5% fat) in early lactation, rising to 27.1% (13.1% fat) in late lactation.

Milk yields were measured by the calf-weighing technique. In well-fed hinds, peak yields of 1400 to 2000 g/day were reached early in lactation. One hind on a restricted food intake gave a maximum of 970 g/day. Lactation continued for 190 to over 280 days. Total yields for the first 150 days were estimated to be 140 to 180 kg in well-fed hinds and 65 kg in the underfed hind.

The feed intakes of the hinds rose during late pregnancy, and in early lactation rose again markedly, to a level about 2.4 to 2.6 times the maintenance requirement of non-breeding animals.

INTRODUCTION

Red deer living in the hills of Scotland are smaller and slower to mature than those in the better environments of lowland deer parks and forests. Puberty is late, mature hinds do not breed every year and there is considerable calf mortality in winter and early spring (Lowe, 1969; Mitchell, 1973). The weights of wild calves are much lower than those of our well-fed captive calves (unpublished data), and it is likely that nutrition is one of the main factors limiting the rate of growth and maturation of wild Scottish deer.

If summer nutrition is sub-optimal, the hind's milk yield may be limited so that calves may grow slowly from birth onwards. Alternatively, the growth check may begin in the autumn when milk yields are declining and the quality of the herbage is also declining rapidly. Weaning is completed between December and March. In order to assess the nutritional status of wild calves, more data are needed on growth in the wild, together with information on the growth potential of well-nourished calves.

As a first step, we have studied the yields and compositions of milk from captive hinds given diets of known composition and amounts. Six hinds were studied,

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four throughout a complete lactation. The terminology used to describe lactation follows that of Cowie & co-authors (1951), but the ability to suckle is restricted to an action of the lactating hind.

MATERIALS AND METHODS

Anatomy of the udder

An udder was taken from a lactating hind shot in July, and frozen. It weighed 550 g. After thawing, a coloured suspension, Colorpaque (Pilot Chemical Co., Ware, Hertfordshire), was injected through the teat canals, two colours being used. The udder was re-frozen and sectioned longitudinally, cutting through the centre of a fore and hind teat, and photographed. The remainder of the udder was divided into a fore and hind quarter, the volumes of which were measured by water displacement.

Table 1. Characteristics of the experimental red deer

<i>Hind no.</i>	<i>Origin</i>	<i>Age (years)</i>	<i>No. of calves</i>	<i>Birth weight (kg) and sex of calf</i>	<i>Hind's post- calving weight (kg)</i>	<i>Rearing and temperament</i>
1970-71						
5	Rhum	3	1	8.0 Male	90	Hand-reared, very tame
6	Rhum	3	1	7.0 Male	90	Hand-reared, tame
1971-72						
8	Rhum	3	1	5.0 Female	75	Caught as adult, fairly tame
10	Hopetoun Park, Edinburgh	6 to 7	4?	6.3 Male	79	Caught as adult, nervous
11	Beinn Eighe	4	2	9.0 Male	92	Hand-reared, tame
12	Whipsnade Zoo	7	1	6.4 Female (Died)	102	Very tame

Animals and management

Six mature hinds were used. All were reasonably tame. Details of the hinds are summarized in Table 1. Records over complete lactations were obtained from all hinds except Nos 6 and 12. The calf of Hind 6 died of accidental injury at 4 weeks of age. Hind 12 had difficulty calving: her dead calf was replaced by a foster-calf but the hind became ill and died in early lactation.

After calving, each hind and her calf were kept together in an indoor pen (3.7 × 1.3 m) except when they were separated for milking or milk recording. The diet of the hinds consisted of dried grass plus a concentrate mixture which formed a quarter to a third of the total food offered. The calves later began to eat some of their dam's food, taking appreciable amounts at 4 to 5 weeks of age, and their combined intakes were recorded. All were given high-plane diets or free access to feed except Hind 10, whose intake was initially restricted to a level sufficient to maintain a non-lactating hind. The calves were weighed at intervals, and studies on their growth will be reported elsewhere.

Milking

The calves were separated from their dams for 6 to 7 hr before milking, and

kept in an adjacent pen. The hinds were milked twice weekly at first, declining to once a fortnight later.

The milk was extracted by machine. A pump set to 380 mm mercury pressure was connected to the udder through a Gascoigne's 'Positive Pulsator' and a bottle for collecting the milk. The teat cup liner had an internal diameter of 1 cm and was 5 cm long. Only one quarter was milked at a time.

The earlier samples from Hinds 5 and 6, which were very tame, were obtained by letting the calf suck for a few seconds to induce milk-ejection (let-down) after which the calf was removed and the hind was milked in a standing position. Hind 5 required little physical restraint, but Hind 6 was more nervous. After the 5th week (Hind 5 only), milk-ejection was induced by injecting 10 units of oxytocin (Pitocin: Parke-Davis, Hounslow, England) into an ear-vein. The animal could be milked 40 to 60 sec after the injection. The efficacy of this method declined and in late lactation, 20 units of oxytocin were needed, with a delay of 8 to 12 min before it took full effect. This increasing difficulty may have been due to adrenalin secretion, as hinds milked under anaesthesia (see below) showed constant high sensitivity to oxytocin throughout lactation.

Three of the hinds used in 1971–72 (8, 10 and 11) would not tolerate machine milking. They were therefore immobilized by intramuscular injection of etorphine/acepromazine ('Immobilon, Large Animal' (1 ml/100 kg body-weight): Reckitt & Colman, Hull, England). When the hind was lying down, 10 units of oxytocin were injected into the jugular vein and she was milked. After milking, the antagonist ('Revivon') was injected intravenously, and the animal stood within 1 to 4 min. This procedure was repeated up to seventeen times per animal without apparent ill-effect, other than a slight loss of appetite for 24 to 48 hr afterwards, and without any appreciable change in sensitivity to the drug. It is not possible to tell if the drug had any effect on milk yield or composition, but the peak yields and composition of milk from animals milked in this way were not markedly different from those for which anaesthesia was not used.

Usually either two quarters (one fore and one hind) or, later, all four quarters of the udder were milked out completely, to obtain representative samples. The volume of milk was recorded and, knowing the time for which the calf had been separated and the number of quarters milked, it was possible to calculate an approximate 24-hr secretion rate, for comparison with the yields estimated by the calf-weighing technique described below. The milk obtained presumably included much of the milk present in the udder at the time when the calf was taken away, and the calculated yields may well have tended to overestimate milk production at times when the calf was sucking infrequently.

The samples for analysis were stored at -20°C .

Measuring the milk intakes of the calves

The calves of Hinds 5 and 6 were watched when 8 to 9 days old. From 09.00 to 19.00 hours, each sucked four times. For the intake measurements, we allowed the calves to suck their dams five to six times in 24 hr at first (night interval not more than $6\frac{1}{2}$ hr) falling to four times at 120 days (night interval 6 to 10 hr) and three times from 150 days onwards. In 1970–71, the yield from

Hind 5 became too small to measure accurately after 160 days and the time of weaning was not established exactly. In 1971–72, lactation ceased completely in Hind 11 at 190 to 200 days, but Hinds 8 and 10 were still producing a little milk when the study was terminated at 275 and 282 days after parturition, respectively.

Before and after sucking, the calves were weighed on a machine (Model 565, John White & Sons, Auchtermuchty, Fife) weighing to 100 kg, having a scale reading to ± 1 kg in 25 g divisions. With these very tame calves, weights could be determined to ± 10 to 15 g. Precision of weighing therefore permitted an accuracy of about 5% for estimates of 24-hr yield in early lactation, falling to ± 10 to 20% in late lactation, when yields were low.

When put in with their dams, all except Hind 10's calf were immediately accepted by their mothers. After the calf ceased to suck, it was removed and re-weighed. If no attempt was made to suck within about 15 min, the calf was removed and a missed feed was recorded. Hind 10, given a restricted amount of feed, had little milk, was also rather nervous, and was clearly not able to satisfy her calf. The calf made sustained efforts to get milk, and was often rejected at first, although it was sometimes allowed to suck if left alone with its dam for 10 min. The method used probably underestimated the milk production of this animal, and may have underestimated some of the others in late lactation. Hind 10's calf grew slowly, and was given creep feed from 29 days of age.

One difficulty with the method is the risk of the calf defaecating or urinating while sucking. This is especially likely in very young calves in response to being licked by the dam, who then consumed the faeces and urine (Arman, 1974). To prevent this, the calves were fitted with 'nappies' made out of soft sacking furnished with four leg-holes and a pad of cotton wool to absorb the urine, and pinned together with blanket pins. Hind 8, however, would not then accept her calf. We therefore wiped her female calf's perineal area with warm, wet cotton wool in an attempt, usually successful, to induce excretion before weighing.

Analysis of milk

All the individual samples of milk were analysed for the major constituents (total solids, fat, total N, lactose, ash). Composite samples, made by mixing together portions of the individual samples in proportion to the yields at the same stage of lactation, were also made for the periods: (a) 3 to 30 days (early lactation), (b) 31 to 100 days (mid-lactation) and (c) 101 days onwards (late lactation). These composite samples, plus any samples of colostrum or 2nd-day milk available (twenty samples in all), were analysed not only for major constituents but also for nitrogenous fractions, minerals, and gross energy content.

The fat content of the milk was measured by the Gerber method (British Standard 696, Part 2: 1969). A suitable weight of milk was introduced into the butyrometer and water was added to 11 ml. The fat content was calculated according to the equation:

$$\% \text{ fat} = 11.22 \times \text{butyrometer reading/weight of milk used.}$$

Lactose was determined in the 1970–71 samples by the colorimetric method

of Marier & Boulet (1959), and in the 1971–72 samples by the method given in British Standard 1741 (1963). Total solids and ash were also determined by the methods of British Standard 1741. Total nitrogen was estimated by an automated Kjeldahl method (Davidson, Mathieson & Boyne, 1970). Non-protein nitrogen was estimated after precipitation of protein with 15% trichloroacetic acid, and non-casein nitrogen after precipitation of casein by adjusting the milk to pH 4.6 in an acetate buffer (Ling, 1944): the corrections for the volumes of precipitates were altered where necessary to allow for the higher solids content of deer's milk. From the figures obtained, protein N (total N–non-protein N), casein N (total N–non-casein N) and albumen+globulin (whey-protein) N (non-casein N–non-protein N) could also be calculated. All nitrogen figures were multiplied by 6.38 to convert to protein, although the validity of this factor has not been established for deer's milk.

Chloride was measured by the method of Ling (1944). Calcium was measured on a 1:20 dilution by the method of Gitelman (1967). It was found that some phosphorus was lost when the milk was ashed. To avoid this loss, 5 g milk was ashed with 3 ml of 3% calcium acetate solution. The ash was dissolved in 10 ml hot 2.5 M-HCl and made up to 100 ml with water. This ash solution was used for the estimation of Na and K by flame photometry (Evans Electro-selenium, Model A), of Mg by atomic absorption spectroscopy in strontium chloride solution, 6.5 g/litre, and of P using the molybdate-vanadate reaction in a Technicon auto-analyser.

The calorific values of the milks were determined on 5-g samples, which were freeze-dried before combustion in an adiabatic bomb-calorimeter.

RESULTS

Gross anatomy of the udder

The udder has four quarters, each with a single teat-canal. The udders of deer in early lactation weigh 500 to 1300 g (Mitchell, 1973). Plate 1 is a photograph of a sectioned udder, showing the fore and hind quarters, and the small milk cisterns. The two quarters which were dissected out had volumes in the ratio of 1 (fore-quarter) to 2.4 (hind-quarter).

Milk yields

The calves took about 150 to 630 g of milk per feed, and this was consumed within $\frac{3}{4}$ to 4 min. After about 65 days, the calves became less eager to suck and their mothers less patient, and occasional feeds were missed. From 90 to 140 days onwards, more feeds were missed and the amount taken fell to 50 to 250 g per feed. Parturition and maternal behaviour have been described by Arman (1974).

The recorded milk yields for the four complete lactations are shown in Text-figs 1 and 2. The yield in kcal gross energy/day follows a different curve from that expressed in g/day owing to the changes in milk composition. For three of the deer, the graphs also show the yields in g/day estimated from the amounts of milk obtained by machine milking. These, with a few exceptions, provide support for the values obtained by the calf-weighing technique over

the main part of lactation, but, as expected, tend to be a little higher. There were, however, two periods during which the yields of some deer calculated from milking were markedly higher than those obtained by the sucking calf. These two periods were: (i) the onset of lactation, when it appeared that a very young calf could not always consume all the milk its dam produced, and (ii) late in lactation, at 150 to 200 days, at the onset of the very gradual weaning

TEXT-FIG. 1. Milk yields of red deer. ●, Yield estimated by calf-weighing (g/day); ○, yield estimated by calf-weighing (kcal/day); x, approximate yields from milkings (g/day).

process, when the calf either did not want or was not allowed to suck its mother dry. From watching the behaviour of the animals, it was impossible to say whether the calf or its mother dictated the onset and pace of weaning.

The peak yields, by weight, and their calorific values, and the estimated total yields to 150 days, are given in Table 2. The lactation curves were of three types: (i) where lactation remained at its initial high level for 2 to 3 months, as in Hinds 5, 8 and 12; calves sucking these hinds grew quickly, (ii) where yields started to decline in the first month, as in Hinds 6 and 11, and (iii) where lactation was poor and erratic, as in Hind 10, which was given a restricted diet; her calf grew slowly.

FIG. 1. Longitudinal section of a red deer udder.

FIG. 2. Radiograph of a red deer udder. Left hind-quarter completely filled and right fore-quarter partly filled with radio-opaque material.

(Facing p. 73)

TEXT-FIG. 2. Milk yields of red deer. ●, Yield estimated by calf-weighing (g/day); ○, yield estimated by calf-weighing (kcal/day); x, approximate yields from milkings (g/day).

Table 2. Peak and cumulative milk yields from red deer hinds

Hind no.	Diet (see Table 3)	Time of peak (days after calving)	Peak yield (g/day)	Calorific value of peak yield (kcal/day)	Total to 150 days (kg)
5	High plane	36	1955	2450	180
6	High plane	6	1435	1850	—
8	Free feeding	17	1415	1850	140
10	Low plane	17, 60	970, 750	1550	65
11	Free feeding	7	1870	2600	160
12	Free feeding	14	1980	2400	—

Food intake in relation to the hind's weight and milk yield

After calving, the food intake of the well-fed hinds increased greatly, and in spite of the heavy demands of lactation they gained 7 to 12 kg in 20 to 30 days. The initial weight gained was slowly lost until at about 200 days the weight was nearly the same as it was after parturition.

From our records over a number of years, we are able to estimate the feed required for maintenance of body weight in non-breeding deer. Table 3 gives our estimates of the maintenance needs of the hinds used, at their post-calving weights, together with data on their actual food intakes. In late pregnancy, the hinds fed according to their appetite ate 1.2 to 1.8 times the maintenance needs of non-breeding animals of similar weight, rising to 2.4 to 2.6 times maintenance needs in early lactation. Hinds 5 and 6 were rationed at 1.6 to 1.8 times maintenance needs during the main part of lactation, and appeared to lactate about as well as those fed according to appetite. Hind 10 was kept on a restricted diet at about the maintenance level, was in poor condition at calving and lost 8.5 kg up to the 43rd day of lactation. Her milk yield started at a low level and then fell still further: the calf grew very slowly and had to be given creep feed. The hind's ration was increased on the 32nd day to 1.5 times the maintenance needs and her milk yield showed a rapid response, rising to a small peak about Day 60. She did not start to gain weight immediately, and it seems that milk production took a degree of priority over the hind's own condition. As lactation declined, her condition improved and by Day 200 after calving she had regained her post-calving weight. This hind suffered a uterine prolapse at parturition (Arman, 1974) and although treatment was immediate and successful, it is possible that the mishap affected her lactation to some extent.

Milk composition

Tables 4 and 5 show the analytical results for the composite samples of milk representing early, middle and late lactation, and also those of the samples taken in the first 2 days of lactation. Hind 12 has been omitted from the mean values as she was ill and later died.

Only one sample was obtained immediately after calving (Hind 8). The colostrum had a very high solids content (34.4%), its fat content was higher than normal and the main difference from normal milk lay in the content of whey proteins (12.7%, against a normal 1.1%). A 15-hr sample (Hind 11) contained only 3.4% whey proteins and a 21-hr sample (Hind 12) only 2.5%. The transition from colostrum to normal milk thus occurred very rapidly, and was completed by the 3rd day.

The calorific values obtained for the milk by bomb calorimetry are in general agreement with values calculated from the analytical results according to the formula derived by Perrin (1958b) for ewe's milk. With only three exceptions, the values calculated according to his formula are within ± 8 kcal/100 g milk of the values obtained directly.

The milk of the red deer is very rich, and the concentration of total solids increased as lactation advanced. In order to study the variation in composition, the 102 individual analyses were grouped into nine periods as follows: 2 to 20, 21 to 40, 41 to 60, 61 to 80, 81 to 120, 121 to 160, 161 to 200, 201 to 240 and

Table 3. Food intakes of pregnant and lactating red deer

Hind no.	Post-calving weight (kg)	Weight change after calving	Calculated maintenance requirement (g dry matter/day)	Dry matter intakes (g/day)	
				Before calving	After calving
5	90	Not recorded	1700	1800 (-45 days) 2000* (-5 days)	2200* (+5 days) 3050* (+16 days on)
6	90	Not recorded	1700	1950 (-60 days) 2050* (-58 days on)	2700* (+12-30 days)
8	74	Gained 7 kg to +75 days then lost 7 kg to +200 days	1450	1300* (-50 days) 2650 (-30 days) 2100 (-5 days)	3000 (+4 days) 3500 (+20 days) 2550 (+30 days)
10	79	Lost 8.5 kg to +43 days then gained 7.5 kg to +210 days	1500	1450* (-18 days on)	1450* (to +31 days) 1800* (+32 to 41 days) (Calif creep fed)
11	92	Gained 12 kg to +31 days then lost 12 kg to +185 days	1700	1900 (-12 days) 2900 (-2 days)	4350 (+10 days) 4000 (+30 days)
12	102	(III; died)	1850	1950 (-150 days) 2400 (-110 days) 2400 (-25 days) 2250 (-5 days)	—

* Not fed according to appetite.

Table 4. Gross composition of red deer milk*

Hind no.	Stage of lactation (days)	Total solids	Fat	N × 6.38	Casein N × 6.38	Non-casein N × 6.38	Whey-protein N × 6.38	Non-protein N × 6.38	Lactose	Gross energy (kcal/100 g milk)
5	Day 2	18.7	6.00	6.76	4.85	1.91	1.51	0.40	4.88	—
	3 to 30	19.4	6.80	6.96	5.62	1.34	1.08	0.26	4.66	112
	31 to 100	23.3	10.10	7.52	6.07	1.45	1.30	0.15	4.72	139
	101 to 175	27.7	13.50	8.23	6.65	1.58	1.42	0.16	4.55	191
6	Day 2	19.0	6.65	6.79	—	—	—	—	4.81	—
	3 to 30	21.4	9.30	6.59	5.17	1.42	1.06	0.36	4.68	140
	Colostrum	34.4	11.05	18.38	5.40	12.98	12.67	0.31	4.03	215
8	Day 2	19.4	7.10	7.40	5.02	2.38	2.03	0.35	3.81	114
	3 to 30	21.2	8.40	7.32	5.87	1.45	1.25	0.20	4.42	131
	31 to 100	23.4	10.00	7.98	6.35	1.63	1.42	0.21	4.42	150
	100 to 254	27.0	12.20	9.63	8.04	1.59	1.40	0.19	4.35	179
10	3 to 30	21.3	8.25	7.91	6.60	1.31	0.89	0.42	3.89	134
	31 to 100	24.2	11.55	7.42	6.07	1.35	0.99	0.36	4.52	159
	101 to 261	27.4	14.20	8.20	6.52	1.68	1.39	0.29	4.41	189
	Day 1	25.8	10.65	9.06	5.44	3.62	3.39	0.23	4.90	145
11	3 to 30	22.2	9.70	6.91	5.30	1.61	1.34	0.27	4.48	131
	31 to 100	23.0	9.75	7.62	6.18	1.44	1.21	0.23	4.14	155
	101 to 187	26.2	12.55	8.30	6.85	1.45	1.20	0.25	4.52	180
	Day 1	20.5	6.65	8.64	5.68	2.96	2.50	0.46	4.44	109
	3 to 25	23.9	11.95	6.85	5.36	1.49	1.22	0.27	3.83	160
Means (excluding Hind 12)	3 to 30	21.1	8.5	7.14	5.71	1.43	1.13	0.30	4.45	130
	31 to 100	23.5	10.3	7.63	6.16	1.47	1.23	0.24	4.45	156
	101 +	27.1	13.1	8.59	7.03	1.56	1.34	0.22	4.46	185

* Values expressed in terms of g/100 g milk.

Table 5. Mineral composition of red deer milk*

Hind no.	Stage of lactation (days)	Ash	Ca	P	Mg	Na	K	Cl
5	Day 2	1.11	0.23	0.23	0.018	0.038	0.15	0.092
	3 to 30	1.15	0.28	0.23	0.020	0.037	0.13	0.079
	31 to 100	1.06	0.25	0.18	0.019	0.030	0.11	0.083
	101 to 175	1.04	0.26	0.18	0.021	0.034	0.10	0.090
6	Day 2	1.07	0.23	0.23	—	—	—	—
	3 to 30	1.20	0.28	0.22	0.017	0.038	0.12	0.078
8	Colostrum	0.97	0.27	0.21	0.025	0.046	0.14	0.119
	Day 2	1.16	0.19	0.24	0.019	0.038	0.15	0.082
	3 to 30	1.20	0.23	0.22	0.017	0.038	0.13	0.080
	31 to 100	1.13	0.19	0.16	0.014	0.040	0.14	0.065
	101 to 254	1.11	0.25	0.20	0.020	0.046	0.15	0.107
10	3 to 30	1.10	0.15	0.21	0.020	0.029	0.12	0.061
	31 to 100	1.08	0.18	0.20	0.020	0.034	0.13	0.061
	101 to 261	1.09	0.23	0.19	0.023	0.037	0.12	0.061
11	Day 1	1.13	0.18	0.23	0.015	0.016	0.08	—
	3 to 10	1.25	0.16	0.20	0.019	0.015	0.10	0.052
	31 to 100	1.17	0.26	0.19	0.020	0.025	0.13	0.069
	101 to 187	1.17	0.26	0.19	0.023	0.025	0.12	0.062
12	Day 1	1.02	0.20	0.21	0.023	0.041	0.18	0.102
	3 to 25	1.20	0.29	0.21	0.018	0.029	0.14	0.089
Means (excluding Hind 12)	3 to 30	1.18	0.22	0.22	0.018	0.033	0.12	0.070
	31 to 100	1.11	0.22	0.18	0.018	0.037	0.13	0.071
	101 +	1.10	0.25	0.19	0.022	0.035	0.12	0.080

* Values expressed in terms of g/100 g milk.

241 to 282 days. An analysis of variance was carried out for each hind to discover whether the variation between periods was greater than that within periods, and to test for significant trends with time and for significant differences between animals.

Lactose and ash concentrations did not change significantly during lactation, although there were significant differences between animals ($P < 0.001$). The mean values in g/100 ml were: Hind 5: 4.7 and 1.09; Hind 8: 4.2 and 1.13; Hind 10: 4.1 and 1.13; and Hind 11: 4.5 and 1.20.

The concentrations of total solids, fat and protein all changed significantly with time, and these changes are illustrated in Text-figs 3, 4 and 5. The general tendencies were for total solids to rise from about 21% to 28% over the first 140 days and then remain constant; for fat to rise from about 7 or 8% to about 13% over 140 days and then to level off or fall slightly; and for protein to rise slowly from about 7% to 9% over 180 days. Non-protein nitrogen, on the other hand, tended to fall slightly. These changes are reflected in the gross energy value of the milk, which rose markedly. There were significant differences between animals in the case of fat ($P < 0.01$) and protein ($P < 0.001$). The underfed Hind 10 gave milk with a low protein content at certain periods, particularly early in lactation. Within these general trends, there was considerable variation, particularly in fat content, between samples from the same animal in

TEXT-FIG. 3. Change in solids content of red deer milk during lactation. ●, Hind 5; ○, Hind 8; ▲, Hind 10; △, Hind 11.

TEXT-FIG. 4. Change in fat content of red deer milk during lactation. ●, Hind 5; ○, Hind 8; ▲, Hind 10; △, Hind 11.

TEXT-FIG. 5. Change in total protein content of red deer milk during lactation. ●, Hind 5; ○, Hind 8; ▲, Hind 10; △, Hind 11.

the same periods of lactation. For the milk of individual hinds within lactation periods, the residual standard deviations were 1.7 for total solids and 1.3 for fat contents.

DISCUSSION

Milk composition in deer and other ungulates

Little is known of the composition of the milk of wild ungulates. In addition to the values for deer discussed below, results for other species are reviewed by Jenness & Sloan (1970). Van Zyl & Wehmeyer (1970) reported analyses for some antelope, Treus & Kravchenko (1968) described studies on domesticated eland (*Taurotragus oryx*), and Cook, Pearson, Simmons & Baker (1970) on the milk of Dall sheep (*Ovis dalli dalli*). From work on domesticated animals, it is known that representative samples are obtained only when the udder is completely emptied and when the animal is being regularly milked or is suckling. In the case of the red deer, in spite of careful milking techniques, there was still considerable variation between successive samples from the same animal, as well as major changes in milk composition during lactation. Many of the published figures for wild species are based on analyses of a single or only a few samples, in some cases taken from animals which were not fully milked out (or even from dead animals), often at unknown times after parturition. These give no more than a very general idea of milk composition, and can be misleading.

Some published values for the composition of milk from various species of deer are summarized in Table 6. Analyses of red deer milk have been reported once previously (Ben-Shaul, 1962) for the first 2 days of lactation only, and these are consistent with our own results (Table 4). All deer produce very rich milk, and that of the reindeer is outstandingly rich. When samples were taken at different stages of lactation, a common feature was the great increase in concentration of solids, particularly of fat, as lactation advanced. This has already been noted by Aschaffenburg, Gregory, Kon, Rowlands & Thompson (1962) and is probably a feature of Cervidae. The change in composition appears to be greater than in most Bovidae, although data on wild bovids are too few to tell whether this characterizes wild as opposed to domesticated species, or whether there is a real difference between the two families. The secretion of very rich milk, and the ability of the offspring to suck very rapidly, would clearly be advantageous to any species subject to predation, provided water is available to the young.

The most relevant domesticated animal to compare with deer is perhaps the sheep because it is of similar size and has not been selected for milk production as much as cattle and goats. Jenness & Sloan (1970) summarize the average composition of ewe's milk as 19.3% total solids, 7.4% fat, 5.5% protein and 4.8% lactose. The concentrations of fat and protein are rather higher in the milk of red deer than in ewe's milk, but that of lactose is similar. The ash content of deer milk is quite high, the amounts of calcium and phosphorus being greater than in ewe's milk, although chloride is lower. In ewes, there is some variation during lactation. Corbett (1968) found an initial fall in fat and protein in the first 2 weeks, followed by a rise to the end of lactation. Barnicoat, Logan & Grant (1949), and Perrin (1958a) found a similar rise in late lactation. Cook, Pearson, Simmons & Baker (1970) reported an even greater rise (from 13 to 20% fat) in wild Dall sheep.

Milk yields

Our knowledge of the milk yields of wild ungulates is rather scanty. Varo & Varo (1971) milked wild reindeer, after separation from their calves, and calculated their daily yield to range from 47 to 206 ml/24 hr. The authors acknowledge, however, that owing to technical difficulties and the effects of forcible restraint, these surprisingly low values may be underestimates, and they are clearly inconsistent with the growth rates of reindeer calves. Yazan & Knorre (1964) working with hand-milked domesticated elk (*Alces alces*) in Russia, obtained yields of 2 to 6 litres per day. Treus & Kravchenko (1968), who studied domesticated eland (*Taurotragus oryx*) which had been maintained as a dairy herd in Russia for many generations, recorded maximum yields of 0.9 to 7.0 kg/day.

There are two recognized methods for estimating the milk yields of domesticated animals with their offspring at foot.

(a) By removing the offspring and milking the dam out after an injection of oxytocin, and again milking her out after a known period (e.g. 4 hr): the amount obtained at the second milking is used to calculate the 24-hr yield.

(b) By allowing the mother to suckle her offspring at set intervals during

Table 6. The composition of milk in some cervids

Species	Stage of lactation	No. of samples	% solids	% fat	Source
Red deer (<i>Cervus elaphus</i>)	Colostrum 2 days	?	34.1	19.7	Ben-Shaul (1962)
	'Milk'	?	23.8	9.2	Jenness & Sloan (1970) quoting Ben-Shaul (1962)
			34.1	19.7	Present study
Sika deer (<i>Cervus nippon</i>)	Colostrum 3 to 30 days	1	34.4	11.0	
	31 to 100 days	100	21.1	8.5	
	100 days +		23.5	10.3	
			27.1	13.1	
Sika deer (<i>Cervus nippon</i>)	?	?	36.1	19.0	Ben-Shaul (1962)
Fallow deer (<i>Dama dama</i>)	?	1	25.3	12.6	Ben-Shaul (1962)
Roe deer (<i>Capreolus capreolus</i>)	?	?	—	6.7	Ben-Shaul (1962)
Reindeer (<i>Rangifer tarandus</i>)	Early	1 Mixed	22.2	9.2	Aschaffenburg <i>et al.</i> (1962)
	Middle	1 Mixed	33.1	16.9	
	1 to 9 weeks	7	—	15.1	Berge (1963)
	8 to 15 weeks	6	—	24.7	
	25 to 30 days	5	27.2	10.8	Luhtala, Rautainen & Antila (1968)
	30 to 40 days	14	27.8	13.1	
	40 to 50 days	8	31.5	16.3	
	50 to 60 days	8	32.0	16.0	
	80 to 100 days	7	40.9	21.6	
	100 to 120 days	5	38.1	19.6	
Caribou (<i>Rangifer arcticus</i>)	Colostrum 4 days	1	40.4	23.2	Hatcher, McEwan & Baker (1967)
		1	31.8	16.9	
Moose (elk) (<i>Alces alces</i>)	'Average'	?	—	10	Yazan & Knorre (1964)
	?	15	21.5	10.0	Ivanova (1964)
	2 to 3 weeks 2 months	1 Dead 1 Dead	24.8 24.9	3.9 10.5	Cook, Rausch & Baker (1970)
White-tailed deer (<i>Odocoileus virginianus</i>)	2 days	1	22.1	8.0	Silver (1961)
	7 days	1	23.1	8.0	
	1 month	1	22.2	7.5	
	5 months	1	33.5	18.0	
	1 to 21 days	34	24.1	9.5	Youatt, Verme & Ullrey (1965)
Mule deer/black-tailed deer (<i>Odocoileus hemionus</i>)	Early	?	—	8.3	Hagen (1951)
	Mid-late Early	3 Dead 3 (1 Dead)	20.8 to 27.6 25.0	8.1 to 13.6 10.4	Browman & Sears (1954) Kitts, Cowan, Bandy & Wood (1956)

24 hr (or less) and recording milk yield as the gains in weight by the offspring during the suckling periods.

The two methods do not always give similar results, the first method estimating potential production and the second actual production. The techniques used with sheep, and their limitations, have been discussed by Barnicoat *et al.* (1949), Munro & Inkson (1957), Coombe, Wardrop & Tribe (1960), and by Poulton & Ashton (1972). We decided to use the second method since we were primarily interested in calf nutrition.

Bubenik (1965) found that red deer calves at 12 to 15 days of age sucked six times in 24 hr, falling to 1 to 3 times at 3 to 4 months, and our own observations agree with this. Bubenik found the sucking periods averaged 100 sec in duration, with an average milk intake per period in the first 4 weeks of 370 ml. Lambs suck rather more frequently (Ricordeau, Boccard & Denamur, 1960; Ewbank, 1967). Wallace (1948) found that lambs could drink a 4-hr milk production at one sucking, and Munro & Inkson (1957) found no difference in the yield of ewes when measured by 1- and 4-hr suckings. Louca (1972) found the milk yields of ewes to be the same when their lambs were with them for 12 or 24 hr a day, and the length of the overnight interval may not be critical. The technique we used, letting the calves suck six times in 24 hr at first, decreasing later, probably allowed them to take in as much milk as they could in 1 day.

The maximum daily yields of our well-fed hinds ranged from 1415 to 1980 g/day (Table 2, Text-figs 1 and 2). In volume, these yields are similar to those from well-nourished (but smaller) ewes (Barnicoat *et al.*, 1949; Peart, 1968; Wilson & co-authors, 1970). In energy terms, yields by our deer are higher than for sheep and were consistent with the observed growth rates of the calves (to be reported elsewhere). Our hinds, except Hind 8, were rather larger than most wild Scottish hinds and the potential milk production of wild deer, even when well-nourished, might well be lower. In Czechoslovakia, Bubenik (1965) estimated the milk yields of red deer to be 3.0 to 4.5 litres per day, a much higher figure than our own. The birth weights and growth rates of Czechoslovak deer are also greater than those of Scottish ones (Bubenik, 1959), and the yields estimated by Bubenik are consistent with the growth rates of his deer calves.

The shapes of the lactation curves of deer and sheep are similar (Barnicoat *et al.*, 1949), each having an early peak and long duration (180 to 250 days or more). Even the hind on restricted food intake (Hind 10) continued to lactate for the normal length of time.

The food intakes of the deer fed according to their appetite rose markedly after calving, and at first were sufficient to sustain lactation and provide for an increase in body weight. The maintenance needs of deer are higher than those of sheep, and they appear to have a relatively higher fasting metabolic rate (Brockway & Maloiy, 1968). The increase in voluntary intake during lactation was similar to, or a little lower than, that of sheep kept indoors (Weekes, 1973) and the hinds' intakes reached very high levels (2.4 to 2.6 times the maintenance needs of non-lactating animals of the same weight). In the wild, the peak of lactation occurs in summer when the available herbage is abundant and of high quality and, thanks to their good appetite, hinds may be able to sustain

high milk yields even though undernourished at other times of the year. The poor lactation in our one underfed hind emphasizes that lactational performance may be severely affected if sufficient good food is not available. The hind, with the small fat reserves characteristic of wild ungulates, is probably unable to emulate the dairy cow's ability to produce milk 'off her back'. More information on calf growth in the wild is needed to establish how frequently poor lactation does retard calf development. In October, wild hinds which have been lactating are in poorer condition and show a lower fertility rate than non-lactating ('yeld') hinds (Mitchell, 1973) and this indicates that even in summer, the hinds may not always be able to eat enough both to lactate and to achieve breeding condition. It is important that calves are able to grow and attain a good size and condition by October since it is then that there is a sharp fall in the quality of the herbage as well as a declining milk intake, and the calves are subjected to increasing nutritional and climatic stress so that a proportion fail to survive the winter and early spring (Lowe, 1969).

ACKNOWLEDGMENTS

We wish to thank Mr I. McDonald for carrying out the statistical analyses. The deer udder was provided by Dr B. Mitchell and radiographed by Mr G. Wenham. The milking machine was originally made by Dr G. A. Lodge. We would like to thank all those who helped with catching, transporting, rearing and caring for the experimental animals, together with Mr C. B. Lawrence, Mr A. Dalgarno and others for carrying out some of the analyses. We appreciate the many helpful discussions we have had with our colleagues at the Rowett Institute and the Nature Conservancy and their criticisms of the manuscript, and the advice on milk analysis given by Dr J. C. D. White.

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