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The effect of abrupt changes in the concentration and frequency of feeding milk-substitute diets on the voluntary food intake of calves

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1. To examine the relations between short- and long-term regulation of food intake in calves given milk-substitute diets, abrupt changes were made in the dry matter (DM) concentration of the diet (Expt 1) and in the frequency of feeding (Expts 2 and 3).

2. When calves, fed once daily, had the DM concentration of their diet changed, they drank the same volume of milk on the 1st day they received the new diet as they had on the previous days; so the DM intakes changed in proportion to the change in milk DM concentration. Over the subsequent 6 d, milk intake progressively increased when milk DM concentration was reduced. When the DM concentration of milk was increased the volume of milk drunk was reduced to a minimum value 2–3 d after the change in diet and increased thereafter. The size of the changes was dependent on the initial and changed DM concentrations of the milk.

3. In calves receiving milk-substitute diets containing 80–260 g DM/kg, milk intakes were reduced by up to 30% on the 1st day that calves were fed once daily instead of twice daily. Over the subsequent 13 d of once-daily feeding, milk intakes increased, particularly for calves given diets of low DM concentration.

4. Feeding the calves once daily reduced the digestibility of DM in Expt 2 but not the digestibility of crude protein (nitrogen × 6·25) and fat; diets containing lower concentrations of DM were particularly affected.

5. It is concluded that the intake of milk-fed calves at a single meal is regulated by an abomasal stretch mechanism. After an abrupt change in milk DM concentration or in the frequency of feeding, the amount of milk drunk at subsequent meals is modified by some long-term control mechanisms.

Andersson (1972) and Forbes (1980) consider that food intake is regulated by short- and long-term control mechanisms. Short-term control is achieved through the hunger and satiety responses of the animal whilst long-term control is exercised by factors that modify those hunger and satiety responses through a change in either the size of the meal eaten to achieve satiety or the interval between the meals.

The experiments reported in the present paper were designed to differentiate between short- and long-term control mechanisms in the milk-fed calf. In previous experiments (Ternouth *et al.* 1985*a*, *b*), the dry matter (DM) intakes (DMI) of milk-fed calves were found to increase as the DM concentration of the milk-substitute diet was increased. The first experiment described here was designed to examine the intake of calves when the DM concentration of the milk-substitute was changed abruptly every 7 d. In two subsequent experiments the effects on intake of changing abruptly from twice-daily feeding to once-daily feeding were examined.

EXPERIMENTAL

Expt 1. Changes in milk DM concentration

Five Friesian calves (mean birth weight 37·4 kg) were separated from their dams at birth, transported to the calf house, placed in metabolism pens and given 7 litres colostrum in the following 48 h. Starting on the 3rd day, each calf was given one of the five milk-substitute

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Table 1. *Composition of milk-substitute diets given* ad lib. *to calves*

Dry matter concentration (g/kg) ...	80	110	140	170	200	230	260
Quantity of constituents added to water to make 1 kg reconstituted milk							
Skim-milk powder (g)	49·2	67·7	86·2	104·6	123·1	141·5	160·0
Fat-concentrate powder (g)	32·8	45·1	57·4	69·7	82·1	94·4	106·8
Composition of reconstituted milks							
Total solids (g/kg)	76·9	106·1	138·1	166·8	197·0	226·3	252·3
Fat (g/kg)	12·7	19·5	27·8	33·5	40·8	45·3	50·9
Osmolality (mOsm/l)	221	304	409	499	605	708	858

diets *ad lib.* twice daily. The diets were reconstituted to contain 80, 110, 140, 170 and 200 g DM/kg (Table 1) in the same way as those used by Ternouth *et al.* (1985*a*). At 14 d of age, the calves were transferred from twice-daily to once-daily feeding. The calves were given their milk at 08.00 hours and the refusals weighed at 08.15 hours. At 21 d of age and every 7th day thereafter, the concentration of the milk given to each calf was abruptly changed. The order in which the diets were fed to each calf was random, subject to the proviso that the diet fed differed from the previous diet by at least 60 g DM/kg. Thus, the calves were subjected to a total of twelve dietary treatments, each treatment being an abrupt increase or decrease in diet concentration.

The general husbandry of the calves, the methods of feeding and the monitoring of the concentration of DM, nitrogen and fat content of the milk powders and the reconstituted milks were similar to those described by Stobo *et al.* (1979).

Expts 2 and 3. Abrupt change in the frequency of feeding

In Expt 2, five groups of eight calves were given milk-substitute diets containing 80, 110, 140, 170 and 200 g DM/kg. In each group, four calves were given diets reconstituted using fat-concentrate powder and skim-milk powder as shown in Table 1 and four calves were given diets in which the skim-milk powder was wholly or partly replaced by liquid skim milk. For the diets containing 80, 110 and 140 g DM/kg, 10·8 ml liquid skim milk replaced 1 g skim-milk powder but for the diets containing 170 and 200 g DM/kg it was necessary to include 19·7 and 34·4% of the skim milk as powder to achieve the desired DM concentration. Each group of calves was given the diets *ad lib.* twice daily from 2 to 56 d of age and then on day 57 feeding was changed to once daily. This was continued until day 71 when twice-daily feeding was reintroduced. Results for the twice-daily feeding period have been published by Ternouth *et al.* (1985*a*).

The digestibility of the diets was determined using six additional calves; pairs of calves were given the 80, 140 and 200 g DM/kg diets twice daily with faecal collection periods starting at 38 d of age and then once daily starting at 59 d of age. Each experimental period lasted 12 d, with each animal receiving one of the diets reconstituted using either liquid skim milk or skim-milk powder (Table 1). There was a 2 d introductory period followed by a 5 d period of faeces collection. The diet was then changed by substituting liquid skim milk for powdered skim milk, and vice versa within pairs of calves, at the same DM concentration and, after a further 2 d introductory period, faeces were again collected over a 5 d period.

In Expt 3, four groups of eight calves were given diets containing 170, 200, 230 and 260 g DM/kg (Table 1) and subjected to changes from twice-daily to once-daily to twice-daily feeding corresponding exactly to those used in Expt. 2. In contrast to Expt 2, all calves in

Expt 3 were allowed drinking water *ad lib.* for 24 h/d. The final two calves in each dietary group were used to determine the digestibility of the diets commencing on days 63 (once-daily feeding) and 77 (twice-daily feeding) of the experiment. As in Expt 2, faeces were collected for a period of 5 d. Preliminary results for the twice-daily feeding period of the experiment have been published by Ternouth *et al.* (1985*b*).

Analyses of results

In previous experiments, it was found that the DMI of the calves increased with age but decreased with age when expressed as intake/kg live weight $(LW)^{0.75}$ (Ternouth *et al.* 1985*a*, *b*). Consequently, the effects of the experimental treatments were examined after minimizing the confounding effects of age and LW on intake. In Expt 1, the mean intakes of the five calves when given milk of each DM concentration for days 6 and 7 of each 7 d period were analysed to estimate the value of z for which there was no linear dependence of DMI on LW (kg^z). This value of the exponent (z) was 0·82.

In Expts 2 and 3, the intakes for weeks 7, 8, 11 and 12 for each calf were analysed using a similar regression analysis. The calculated values of z were 0·75 and 0·89 respectively. In each case the value of z was calculated from the residual dispersion after elimination of treatment and calf effects. Previous experiments (Ternouth *et al.* 1985*a*, *b*) have shown that offering drinking water reduces DMI of calves given milk-substitute diets of high DM concentrations. As Expts 2 and 3 were conducted over the period between 6 and 12 weeks of age and drinking water was a confounding factor in Expt 3, a standard value of z of 0·75 was used in both experiments. Thus intake values were converted using 0·82, 0·75 and 0·75 as values of z for Expts 1, 2 and 3 respectively.

In Expt 1, the derived intake values were analysed (by analysis of variance) for the immediate change of intake following the twelve changes in concentration. The rate of change of intake in the subsequent 7 d (days 1–7) was calculated for each calf on each treatment and these rates were analysed by analysis of variance. Similarly, the immediate change and subsequent rate of change of intake over the 14 d period following the change from twice-daily feeding to once-daily feeding were analysed in Expts 2 and 3.

RESULTS

Expt. 1. Abrupt changes in milk DM concentration

The calves remained in good health and consumed large amounts of their diets throughout the experiment. As in the previous experiments, the calves had the highest liquid intakes when they were receiving the milk of the lowest DM concentration and the highest DMI when they were receiving the milk of highest DM concentration. The mean DMI of the calves at a mean age of 63 d and LW of 89·7 kg were 36·5, 45·2, 54·3, 65·0 and 64·5 g DM/kg $LW^{0.75}$ for milks containing 80, 110, 140, 170 and 200 g DM/kg respectively. Up to 105 d of age, the mean LW gain of the calves was 0·97 kg/d. When the concentration of DM in the diet given to the calves was reduced, the liquid-milk intake on the 1st day of the new diet was similar to that on the previous day but the DMI was significantly reduced (Fig. 1 and Table 2). Subsequently, the liquid and DM intakes increased. The magnitude of the initial and subsequent changes in intake were dependent on the initial intake and the size of the change in the DM concentration of the diet. When the DM concentration of the milks was increased, the liquid intakes of the calves on the 1st day after the introduction of the new diet were not changed so that the DMI increased in parallel with the change in milk DM concentration. Both liquid and DM intakes were reduced on the 2nd and 3rd days after the increase in diet concentration but generally tended to be increased thereafter (Fig. 1 and Table 2).

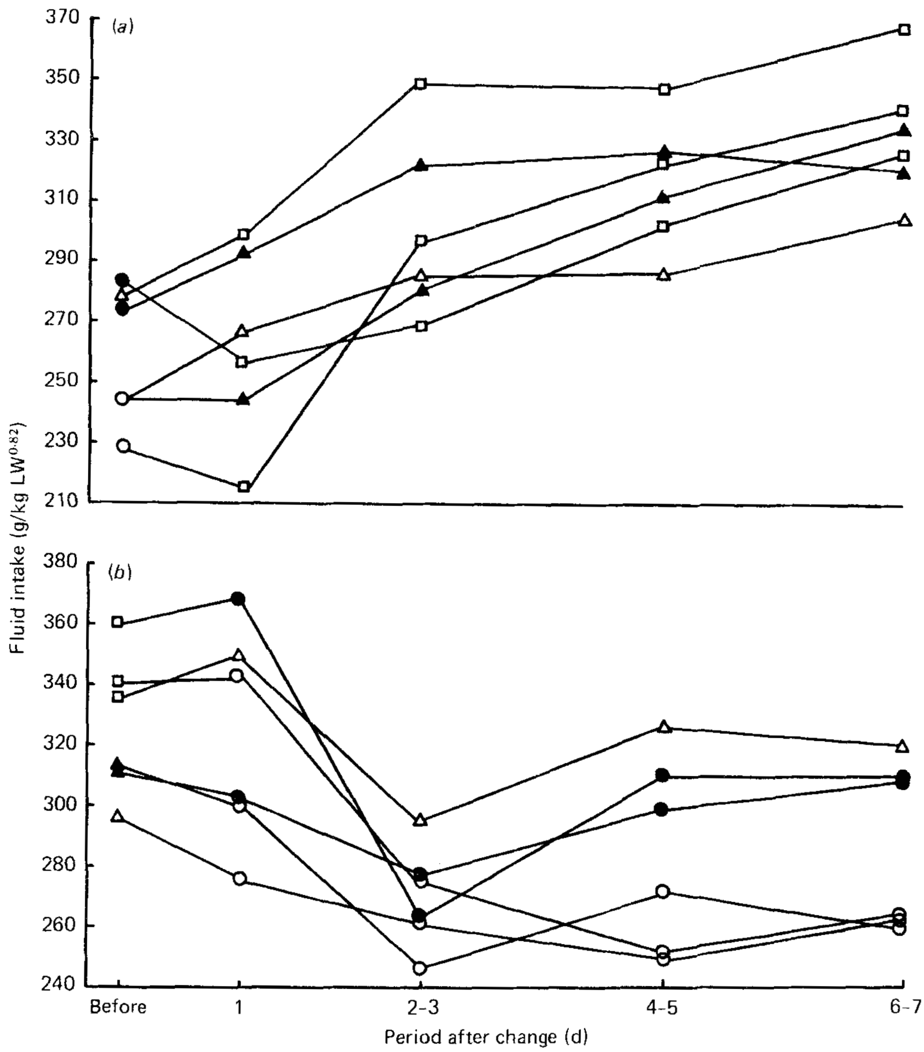

Fig. 1. Expt. 1. Fluid intake (g/kg live weight $(LW)^{0.82}$) of calves before and after an abrupt (*a*) decrease and (*b*) increase in the dry matter (DM) concentration of milk-substitute diets reconstituted at (□), 80; (▲), 110; (△), 140; (●), 170; (○), 200 g DM/kg.

Expts 2 and 3. Changing from twice- to once-daily feeding

In Expt 2, the LW of the calves at 56 d of age were 95·3, 102·4, 104·0, 109·5 and 109·2 kg for the calves given diets containing 80, 110, 140, 170 and 200 g DM/kg respectively. In Expt 3, the corresponding LW were 92·9, 90·3, 103·3 and 104·0 kg for the calves given diets containing 170, 200, 230 and 260 g DM/kg respectively.

The mean intakes for the period 57–70 d of age, when the calves were fed once daily, were 0·73–0·91 of the mean intake when the calves were given milk twice daily. In general, when the calves were given a milk with a lower DM concentration, they were less able to sustain their intakes when transferred to once-daily feeding (Table 3). The intake of drinking-water (Expt 3) did not change significantly when the calves were fed once daily: the mean intakes were 94, 79, 102 and 130 (SE 9·1) g/kg $LW^{0.75}$ for calves offered diets

Table 2. *Expt 1. Mean daily dry matter (DM) intake (DMI; g/kg live weight (LW)$^{0.82}$) before and after an abrupt change in the DM concentration of a milk-substitute diet*

Diet concentration (g DM/kg)		DMI					Rate of change of intake† (g DM/kg LW$^{0.82}$)	SE	Statistical significance of change of intake
			Period after change (d)						
Before	After	Before	1	2–3	4–5	6–7			
200	140	47·9	37·0	39·5	39·5	42·1	+0·83		*
200	110	48·3	26·0	29·9	33·2	35·5	+1·70		***
200	80	45·3	16·6	23·0	24·9	26·3	+1·63	0·40	***
170	110	46·1	31·1	34·2	34·6	33·9	+0·44		NS
170	80	47·5	19·8	20·8	23·3	25·1	+1·00		*
140	80	38·8	23·1	26·8	26·8	28·4	+0·83		*
	Mean	47·7	25·6	29·0	30·4	31·9	+1·07	0·16	***
80	140	25·9	48·4	40·8	45·0	44·1	+0·40		NS
80	170	27·9	61·6	43·7	51·8	51·8	−0·97		*
80	200	26·3	67·6	54·1	49·4	52·0	−2·65	0·40	***
110	170	33·1	50·6	46·2	49·2	51·7	+0·39		NS
110	200	33·2	59·1	48·7	53·7	51·3	−0·91		*
140	200	40·9	54·4	51·7	49·1	51·9	−0·52		NS
	Mean	31·2	57·0	47·5	49·7	50·5	−0·84	0·16	***

NS, not significant.
* $P < 0.05$, *** $P < 0.001$.
† Daily rate of change of intake over the 7 d after the change in milk concentration.

Table 3. *Expts 2 and 3. Mean daily intakes (g dry matter (DM)/kg live weight (LW)$^{0.75}$) of calves given milk-substitute diets following an abrupt change from twice- to once-daily feeding*

Diet concentration (g DM/kg)	Twice-daily feeding†	Period after change to feeding once daily (d)				Rate of change of intake‡ (g DM/kg LW$^{0.75}$ per d)	SE	Statistical significance of change of intake
		1	2–3	6–7	13–14			
80	51·2	35·6	38·3	39·7	41·7	0·39		NS
110	53·4	40·6	42·8	43·2	47·9	0·52		*
140	57·0	46·4	46·4	48·8	51·1	0·40	0·16	NS
170	61·9	51·5	52·4	53·8	57·7	0·49		*
200	61·6	54·7	53·3	56·1	60·1	0·54		*
Mean	57·0	45·7	46·6	48·3	51·7	0·46	0·07	***
170	58·3	52·5	51·4	53·5	53·1	0·10		NS
200	59·5	50·2	53·8	55·2	59·0	0·57	0·23	NS
230	64·9	52·2	52·0	52·9	59·0	0·60		NS
260	61·6	62·4	58·7	60·2	61·2	0·09		NS
Mean	61·1	54·3	54·0	55·4	58·1	0·34	0·12	NS

NS, not significant.
* $P < 0.05$, *** $P < 0.01$.
† Mean daily intake over the 7 d period before the change from twice- to once-daily feeding.
‡ Daily rate of change of DM intake over 14 d period of once-daily feeding.

Table 4. *Expts 2 and 3. Dry matter (DM) digestibility (g/kg) of milk-substitute diets given to calves once and twice daily*

Expt no. ...	2				3			
Diet concentration (g DM/kg)	Twice daily	Reduction when fed once daily	SE	Statistical significance of reduction	Twice daily	Reduction when fed once daily	SE	Statistical significance of reduction
80	963	81·0	18·4	NS	—	—	—	—
140	965	39·0		NS	—	—	—	—
170	—	—		—	942	6·5	11·2	NS
200	949	7·5		NS	942	−3·0		NS
230	—	—	—	—	939	8·0		NS
260	—	—	—	—	940	24·5		NS
Mean	959	42·5	10·6	*	941	9·0	5·6	NS

NS, not significant.
* $P < 0.05$.

containing 170, 200, 230 and 260 g DM/kg respectively. In Expt 2 but not in Expt 3, the digestibility of the DM was reduced when the calves were given milk once daily (Table 4). There were no reductions in the digestibility of N or fat.

In Expt 2, on the 1st day of the once-daily feeding regimen, 24 h after their last meal, the calves consumed 0·70, 0·76, 0·81, 0·83 and 0·89 of their mean daily intake during the previous 7 d when given milk with DM concentrations of 80, 110, 140, 170 and 200 g/kg respectively (Table 3). On days 13 and 14, the corresponding intake values were 0·81, 0·90, 0·90, 0·93 and 0·98; these intakes were significantly higher than on day 1. The changes in intake occurred progressively over the 14 d of the once-daily feeding period. The mean intakes for all diets, 1, 6–7 and 13–14 d after the change to once-daily feeding were 0·80, 0·85 and 0·91 respectively.

In Expt 3, the calves consumed on the 1st day of the once-daily feeding period 0·90, 0·84, 0·80 and 0·91 of the mean intake for the previous week (Table 3). DMI tended to increase over the 14 d of the once-daily feeding period especially at the 200 and 230 g DM/kg milk-substitute concentrations.

DISCUSSION

When the DM concentration of the milk given to the calves was abruptly changed, the calves were unable to perceive the change at the first feed. This indicates that when the calves were drinking, they did not sense the change in composition of the milk as a change in osmolality, density or concentration of a metabolite in the mouth, in the abomasum, in the small intestine or at any other site. Although osmoreceptors and acid-sensitive chemoreceptors which play a role in controlling abomasal emptying have been found in the duodenal mucosa of the calf (Bell & Holbrooke, 1979; Bell, 1980), these receptors appear to have no effect on the intake of milk at a single meal. As the calves were observed to drink for only 3–4 min at a meal it seems unlikely that sufficient glucose was absorbed for an increase in blood glucose concentration to act as a satiety signal and it is thus probable that the intake of milk at each meal was controlled by a physical stretch mechanism. The main organ involved in the regulation of intake appears to be the abomasum as most of the ingested milk accumulates initially in that organ, regardless of the DM concentration of the milk (Hegland *et al.* 1957; Ørskov & Benzie, 1969; J. H. Ternouth, unpublished results).

The abomasum may be considered as an elastic cylinder as it is derived early in embryonic life from a short length of primitive foregut (Warner & Flatt, 1965). This being so, the Law of Laplace for elastic cylinders should apply and the tension around the wall of the abomasum should be proportional to the radius of the abomasum (Hopkins, 1966). Consequently, any increase in the volume of milk consumed will increase the tension in the abomasal wall and may be sensed by tension receptors (Leek, 1972).

When the calves were transferred from twice- to once-daily feeding, the intake on the 1st day was considerably greater than half the intake during the previous day, because the interfeeding interval had been increased from 15 to 24 h. Previous research has shown that when calves are given milk twice daily, a portion of the coagulum has not left the abomasum at the following feeding (Hill *et al.* 1970; Ternouth *et al.* 1975). Thus, when the interfeeding interval was increased to 24 h, additional abomasal capacity must have been available to hold the milk. In addition, the longer interfeeding interval may have resulted in a lower concentration of circulating blood metabolites (for example, glucose) so that long-term control mechanisms controlling food intake may have started to modify the short-term control mechanisms by increasing the degree of abomasal stretch required for satiety to be attained.

In all three experiments, the intakes of the calves were mathematically related to a function of LW, so that changes in DMI were minimized over the whole of each experimental period. In spite of this, in Expt 1, the daily intakes of the calves changed progressively over the 7 d period following each change in diet towards the expected intake for the new milk DM concentration. The greater the change in DM concentration in the milk, the greater the change in intake over the 7 d period. When the frequency of feeding was changed (Expts 2 and 3), greater changes in intake in the subsequent period of 14 d occurred in calves given milks containing the lower DM concentrations. These results suggest that the calves were attempting to optimize their energy intake within the constraint imposed by the physical capacity of the abomasum or some metabolic constraints, possibly the need to excrete water, minerals or metabolic by-products (Dalton, 1967, 1968*a*, *b*; Ternouth *et al.* 1985*b*).

When feeding was restricted to once daily, the calves consumed very large amounts of milk, especially when given the milks containing the low concentrations of DM. When given the milk containing 80 g DM/kg, the intake at a single meal was 16·15 litres, equivalent to 15·8% of LW. These high intakes of milk, at 57–70 d of age, had little effect on the observed incidence of diarrhoea and although small reductions in digestibility were observed (Expt 2), the most substantial reduction occurred in calves given the 80 g DM/kg diet.

It is concluded that in the milk-fed calves, the intake at a single meal is controlled by an abomasal stretch mechanism but that this control is subject to modification by long-term control mechanisms involving an interaction with one or a number of undefined physiological factors.

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