Saliva secretion and its relation to feeding in cattle

3.* The rate of secretion of mixed saliva in the cow during eating, with an estimate of the magnitude of the total daily secretion of mixed saliva

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While ruminants are eating food, saliva is secreted by the parotid, the submaxillary, and the sublingual glands (Colin, 1886; Ellenberger & Hofmeister, 1887; Bailey & Balch, 1961*b*). According to Ellenberger & Hofmeister (1887) the submaxillary glands secrete only during eating and volumes as great as 480 ml in 1 h are produced by these glands in cows. The parotid glands, on the other hand, secrete continuously although their activity is greatly enhanced during the mastication of food (Bailey & Balch, 1961*b*).

By recovering swallowed food boluses from cows and measuring the increase in the amount of water they contained, Colin (1886) and Balch (1958) showed that as much as five parts of saliva could be added to one part of hay though only one part or less was added to one part of fodder beet or succulent green food. During the consumption of certain diets the amounts of saliva secreted exceeded 40 l. in a single day.

Variations in the amount of saliva added to the rumen while different foods are being eaten might have an effect on the subsequent digestion of the food. In the work reported here an attempt was made to clarify the factors that govern the flow of saliva while certain foods are being eaten. In addition, the relationship between the flow of mixed saliva and re-mastication during rumination was studied. From the results of these experiments and those reported earlier (Bailey & Balch, 1961*c*) a preliminary estimate has been made of the total daily flow of saliva.

EXPERIMENTAL

The technique used for measuring saliva secretion during eating was similar to that described by Balch (1958). The amount of saliva added to the food was estimated by collecting and drying representative food boluses. After making allowance for the moisture in the original material the amount of water added to the food was calculated. All swallowed foods arrived in the rumen as discrete boluses which were generally firm enough to be removed intact by hand through rumen fistulas. The mean rate of secretion of saliva was then calculated from the mean rate at which the foods were

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eaten. The findings also allowed an estimate of the average frequency of swallowing food boluses and the average size of bolus.

The cows were generally maintained on the test foods for at least 1 week before experiment. In addition, they were given amounts that were readily consumed in a single uninterrupted period of eating. The amount of digesta in the rumen before each meal did not prevent free access of the hand to the area of the cardia although the position of the digesta frequently required some rearrangement.

Swallowed food boluses were collected in groups of four together, and six groups of four were collected at regular intervals throughout any meal. The mean weight of the boluses in each group was calculated. Values for a single cow receiving a given food were obtained during at least two and usually four or six meals. With succulent foods the moisture contents of the foods were determined at each meal; with drier foods the moisture content was determined once in each experiment. The following foods were investigated in five cows: mangels, dairy cubes, two different samples of fresh grass, dried grass, silage, and two different samples of hay. On two occasions food boluses were collected from one animal during the grazing of succulent young grass. This method of computing the amount of saliva secreted during eating underestimates the quantity of added saliva unless allowance is made for the dry-matter content of the saliva. Since with saliva containing 1 % dry matter the error would be only about 2 %, it has been ignored.

It was of interest to ascertain the effectiveness of saliva in bringing soluble food constituents into solution during ensalivation in the mouth. Swallowed food boluses collected during two meals of hay and one meal of dairy cubes were squeezed by hand and the fluid so obtained was analysed for sodium, potassium, chloride and phosphate. As a measure of the tonicities of the fluids, the freezing-point depressions were also measured. The analytical procedures were those previously described for use with rumen fluid (Bailey & Balch, 1961*a*).

During rumination, representative series of boluses were collected from the animal's mouth either immediately after regurgitation or immediately before re-swallowing. Virtually complete collection was possible by holding the animal's nostrils and recovering the material by hand. These boluses were weighed and the dry-matter contents ascertained by drying to constant weight. The information so obtained allowed some conjecture as to the characteristics of the re-mastication process.

RESULTS

Table 1 lists the mean values for rate of food consumption, rate of saliva secretion and the amount of saliva added to the various foods. The foods were arranged approximately in the order of increasing physical fibrousness. The rate at which food was eaten tended to be highest for the least fibrous foods and lowest for the most fibrous foods. For example, cow A consumed hay 1, which was very fibrous, at a mean rate of 53 g/min but consumed mangels, which were much less fibrous, at a rate of 457 g/min.

The amoun of saliva added to each unit of food varied considerably, the most fibrous foods gaining the most saliva and the least fibrous foods the least. Thus cow A added only 0·16 g saliva to 1 g mangels, but 3·82 g saliva to each g of hay 1. As in the experiments of Balch (1958), there was a tendency for the amount of saliva added to each unit of the more fibrous foods to decline throughout a meal, although it was not so for the less fibrous foods (Fig. 1). With cow A, there was also a definite tendency for the amount of saliva added to a unit of hay to increase again towards the end of the meal.

The rates of secretion of saliva were not obviously related to any characteristics of the various foods and, except with the mangels and grass 2, were very similar for any animal regardless of the food she consumed.

Differences in the dry-matter content of the foods were unrelated to the degree of ensalivation attained in the mouth before they were swallowed. In fact, some foods

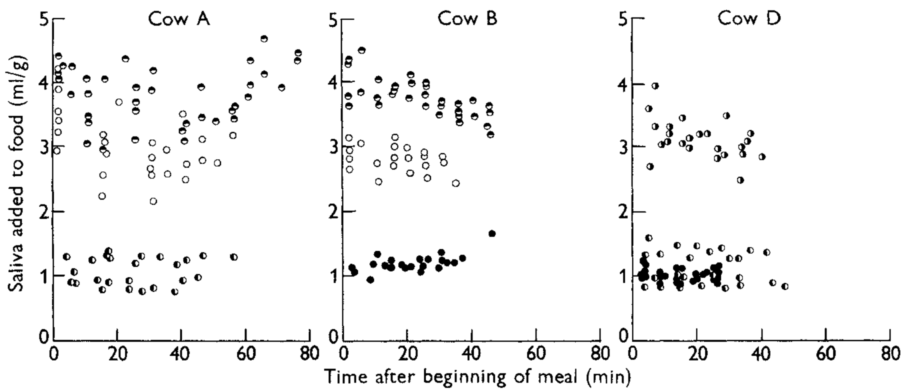

Fig. 1. Amounts of saliva added by cows to foods at intervals after the beginning of eating. ◓, hay 1; ○, hay 2; ◑, dried grass; ◐, freshly cut grass; ●, silage.

Table 1. *Mean values for the secretion of saliva, the rate of food consumption, the weight of food boluses and the frequency of swallowing of the boluses while cows were eating common foods*

Food	Cow	Amount of food eaten/meal (lb)	No. of meals in which boluses were collected	Rate of eating (g/min)	Saliva secreted (ml/min)	Saliva secreted (ml/g food)	Water content of bolus (%)	Weight of bolus (g) Wet	Weight of bolus (g) Dry	Rate of swallowing of boluses (no./min)
Mangels	A	15	4	457·3	73	0·16	92·4	102·3	7·8	4·5
	E	15	4	433·9	145	0·33	92·9	86·5	6·1	5·1
Dairy cubes	A	6	12	356·7	241	0·68	50·1	65·6	12·7	5·5
Fresh grass 2	D	40	4	348·7	196	0·59	87·5	98·4	12·3	3·5
Grazed grass 2	D	—	2	263·8	164	0·62	87·5	73·6	9·2	3·6
Fresh grass 1	A	30	4	241·8	258	1·08	87·9	69·9	8·5	3·3
	D	30	4	258·0	290	1·15	87·3	74·9	9·5	3·5
Silage	B	20	4	201·8	245	1·22	81·1	67·2	12·7	3·0
	D	20	6	294·0	301	1·03	79·7	77·4	15·7	3·8
Hay 2	A	8	6	80·3	238	2·95	79·3	26·9	5·6	3·0
	B	8	6	106·6	297	2·81	78·4	37·6	8·1	2·9
Dried grass	A	8	4	70·5	234	3·36	78·8	28·2	6·0	2·5
	D	8	4	95·3	297	3·12	79·0	35·8	7·5	2·7
Hay 1	A	8	6	52·7	209	3·82	82·6	21·8	3·8	2·4
	B	8	6	79·4	301	3·77	82·6	29·0	5·0	2·8
	C	7	4	32·3	153	4·79	84·8	15·0	2·3	2·2

were drier when they reached the rumen than others were before they were eaten. The dairy cubes contained the least moisture (about 50 %) after being swallowed and most of the other foods contained about 80 % moisture or more.

The weight of food boluses (exclusive of the saliva they contained) and the rate at which they were swallowed increased with increasing rate of food consumption. On average, 80 % of this increase was due to increases in bolus size and 20 % to increases in swallowing frequency (Table 1).

The concentrations of Na, K, chloride and phosphate in the fluid squeezed from the swallowed foods are given in Table 2. For comparison, values, derived from Bailey & Balch (1961 *c*), for the concentrations of the same ions in mixed saliva secreted by cows during rest are included in the table. The depressions in freezing-point of the various fluids are also given. The concentrations of K and chloride in the fluids expressed from hay and from dairy cubes were markedly in excess of the concentrations of the

Table 2. *Composition and depression in freezing-point of the saliva expressed from swallowed dry food compared with the mean composition of mixed saliva secreted by cows during rest*

Activity during collection of sample	Food from which saliva was expressed	Concentration (m-equiv./l.)				Depression in freezing-point (°C)
		Na^+	K^+	Cl^-	HPO_4^{2-}	
Eating	Hay 1	117	141	76	15	0·944
Eating	Hay 2	123	142	61	15	0·985
Eating	Dairy cubes	293	151	127	66	1·460
Resting*	—	133	27	6	33	0·500

* Means for samples collected from five different cows (Bailey & Balch, 1961 *c*).

Table 3. *Weight and dry-matter content of digesta of cows collected from the mouth during rumination, immediately after regurgitation and immediately before swallowing*

Observation no.	Bolus: After regurgitation: Wet weight (g)	Dry-matter content (%)	Before swallowing: Wet weight (g)	Dry-matter content (%)
1	59·4	15·9	34·4	11·0
2	21·9	11·9	40·4	14·1
3	26·9	12·3	12·8	13·4
4	52·8	11·2	28·1	10·3
5	79·3	11·2	12·6	12·7
6	69·5	14·8	17·8	15·2
7	85·1	11·9	15·0	11·3
8	62·3	11·1	23·2	11·2
9	56·2	10·1	9·6	11·5
10	56·2	13·5	15·9	10·1
11	45·8	14·2	11·1	8·1
12	42·7	11·5	28·0	11·4
13	76·9	12·4	—	—
14	55·5	10·6	—	—
Mean	56·5	12·3	20·7	11·7

same ions in mixed saliva secreted during rest. The concentrations of Na and phosphate in the fluid from the dairy cubes were higher than those either in saliva or in the fluid expressed from the hay samples. The concentrations of Na and phosphate in the fluid from the hay were lower than in saliva, possibly because the values for saliva correspond only approximately to the composition of mixed saliva secreted during eating. The tonicities of the expressed fluids were two to three times greater than that of 'resting' saliva. The fluids had a dark-brown colour reminiscent of filtered rumen fluid. The values show that a significant leaching of soluble plant constituents into the saliva occurs during mastication.

During rumination, the mean weight of the regurgitated material collected at the beginning of the periods of re-mastication was nearly three times the mean weight of that collected at the end of the periods, whereas the mean dry-matter percentages were almost the same (Table 3). The appearance and consistency of both sets of samples were identical and were not noticeably altered when the diet of the animals was changed.

DISCUSSION

During eating, the amount of saliva added to foods such as hay was much greater than was added to the same weight of other foods such as concentrates. These experiments confirm and expand earlier observations in this Institute (Balch, 1958), and help to explain the manner in which these variations in the amount of added saliva were brought about.

The amount of saliva added to a given weight of food depends on the rate at which the saliva is being secreted and the rate at which the food is being swallowed; a change in the rate of swallowing could be brought about by increase in either the amount of food in each bolus or in the rate at which the boluses are swallowed.

Considering these possible variables in order, we find that with the foods used in these experiments the mean rate of secretion was 229 ml saliva/min, or two to four times greater than the rate found during rest (Bailey & Balch, 1961*c*). The rate of secretion varied from 108 ml/min with mangels to over 250 ml/min with dairy cubes, certain fresh grass, silage, dried grass and hay. A value of 426 ml saliva/min has been found with ground concentrates (Balch, 1958), but with many foods the rate of secretion seems to lie within the range 200–300 ml saliva/min. The rate of eating varied more markedly, being usually under 100 g/min with hay or dried grass, about 350 g/min with fresh grass and dairy cubes and for one cow reaching 457 g/min with mangels; a difference between hay and dairy cubes was also found in the rate of intake of dry matter. There was a distinct tendency for the rate of swallowing to increase from under three boluses/min with the foods eaten at less than 100 g/min to over five boluses/min with the foods eaten at 350 g/min or faster. This was clearly a less important influence on the amount of saliva added to the food than the mean size of the boluses, which increased from 15–38 g with the foods eaten slowly to 66–102 g with those eaten rapidly; the dry-matter content of the boluses ranged from 2–6 g with the dry roughages, which were eaten slowly, to 33 g with dairy cubes.

The experiments show, therefore, that, although differences in the amount of saliva added to a given weight of certain foods were due partly to differences in the rate of secretion of saliva, variations in the rate of eating appear to be of greater importance. It remains to be shown how and why these changes are brought about and to explain the mechanism by which the act of eating non-fibrous foods results in increased frequency and size of bolus, whereas the eating of fibrous foods has an opposite effect. Though the effects on the bolus can perhaps be explained by the varying physical difficulties in forming boluses from the different foods, the nature of the stimulus for the increased rate of secretion of saliva requires definition.

Table 4. *Amount of water drunk and the estimated amount of saliva secreted daily during eating, ruminating and rest in five cows receiving various diets**

Daily diet	Cow	Water (l.) In food	Water (l.) Drunk	Dry-matter intake (kg)	Saliva secreted (l./day) During eating	Saliva secreted (l./day) During rumination	Saliva secreted (l./day) During rest	Saliva secreted (l./day) Total	Fluid added to rumen (l.) Total	Fluid added to rumen (l.) /kg dry matter	Assumed daily rumination time† (h)
40 lb lucerne silage	B	10	26	7·7	21	50	50	121	157	20	7
	D	11	29	7·7	21	38	39	98	138	18	7
	Mean	11	28	7·7	21	44	45	110	148	19	7
14 lb medium-quality hay	A	1	18	5·5	26	68	52	146	165	30	8
	B	1	18	5·5	26	83	64	173	192	35	8
	C	1	27	5·5	26	64	50	140	168	31	8
	D	1	18	5·5	26	63	48	137	156	28	8
	Mean	1	20	5·5	26	70	56	149	170	31	8
8 lb hay and 12 lb dairy cubes	A	1	22	7·7	17	45	68	130	153	20	5
	C	1	26	7·7	17	39	59	115	142	19	5
	Mean	1	24	7·7	17	42	64	123	148	20	5
2 lb hay, 12 lb flaked maize and 2 lb groundnut cake	A	1	13	6·4	12	18	81	111	125	20	2
	D	1	17	6·4	12	18	75	105	123	19	2
	Mean	1	15	6·4	12	18	78	108	124	20	2
Grass, supplying 12 lb dry matter	A	33	1	5·5	38	62	89	189	223	41	5
	B	35	1	5·5	38	62	90	190	226	41	5
	C	32	8	5·5	38	48	70	156	196	37	5
	Mean	33	3	5·5	38	57	83	178	215	40	5

* Diets used by Bailey & Balch (1961*c*). † See p. 450.

Saliva secretion during rumination. The experiments provided no direct measure of the amount of saliva secreted during rumination. The rate of secretion of parotid saliva during rumination was found, in a steer, to be about 2·5 times the rate during rest (Bailey & Balch, 1961*b*). Since the submaxillary glands are quiescent during rest and rumination (Colin, 1886; Ellenberger & Hofmeister, 1887) it has been assumed, for the purposes of the calculations made in the section that follows, that the flow of mixed saliva during rumination was about 2·5 times the flow of mixed saliva during rest.

The experiments provided a new observation on the act of rumination. As was expected, regurgitation during rumination was rapidly followed by up to four swallows, presumably of surplus fluid. However, during the subsequent period of 40–60 sec in which these digesta were being chewed, the amount of digesta that could be recovered manually from the mouth, and mainly from the tongue, decreased by over 50% although their dry-matter content and appearance remained unchanged. This finding suggests that the material so recovered towards the end of the period of chewing had not been chewed, but that those digesta that had been chewed had passed on into the region between the jaws and the cheek on the chewing side. With the head held in its invariable position during rumination, the parotid papilla seems ideally sited for the high parotid secretion to wash particles from this region of the mouth into the throat. These observations suggest that the material swallowed at the end of a period of chewing consists mainly of unchewed digesta.

Estimation of the total daily production of saliva. Estimates have been made of the amounts of saliva produced daily with five diets studied earlier (Bailey & Balch,

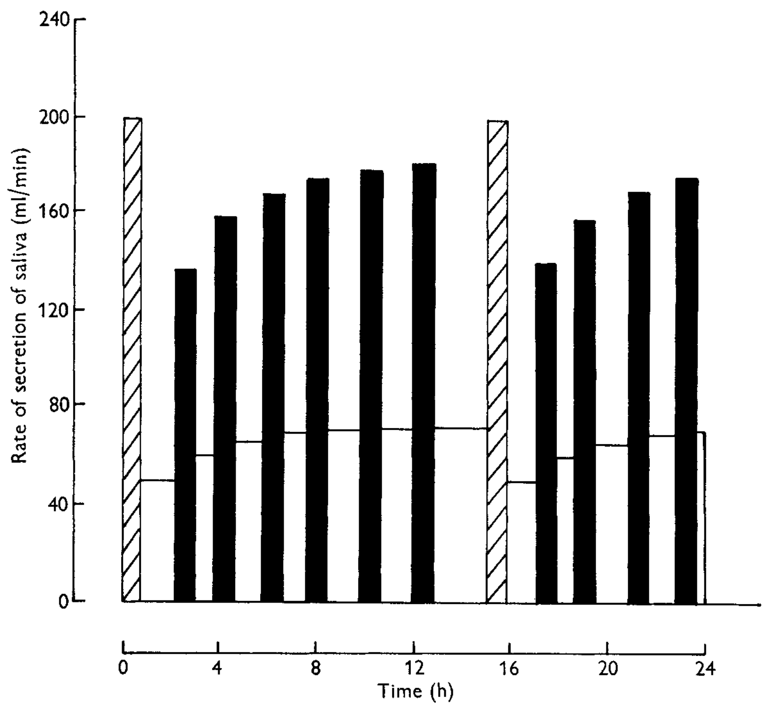

Fig. 2. Diagram representing the pattern of flow of saliva in cows during a period of 24 h. The rate of secretion during eating (hatched bars), ruminating (solid bars) and resting (open bars) is shown.

1961 *c*). The diets are given in Table 4 together with the water drunk and the estimates of saliva production.

Estimates of saliva production during eating were based on the assumption that the rate of secretion was 4·13 ml/g hay, 1·13 ml/g silage, 1·12 ml/g grass, 0·68 ml/g dairy cubes, as found in the experiments described here, and 1·30 ml/g flaked maize (Balch, 1958). The amount of saliva added to groundnut cake was assumed to be the same as that added to flaked maize and ground concentrates.

Estimates of saliva secretion during resting and ruminating were based on the use of histograms of the type shown in Fig. 2. Values for resting were taken from Bailey & Balch (1961 *c*) and values for ruminating were calculated as shown on p. 448. From the observations of other workers (e.g. Johnstone-Wallace & Kennedy, 1944; Balch, Balch, Bartlett, Bartrum, Johnson, Rowland & Turner, 1955; Kick, Gerlaugh, Schalk & Silver, 1937) it was assumed that the periods spent ruminating were as given in Table 4. Errors in assumptions of rates of secretion of saliva and periods of rumination are unlikely to give falsely high final estimates of total daily flow.

By comparison with Table 4 it is clear that earlier estimates for total saliva flow in cattle may have been low. Daily estimates of 56 l. (Colin, 1886), 21 l. (Chrząszcz & Schechtlówna, 1930), 45 l. (Hastings, 1944), 50 l. (Markoff, 1913) and 66 l. (Smith, Kleiber, Black & Lofgreen, 1956) have been made. Support for the values now reported was given by Sperber, Hydén & Ekman (1956) who estimated that 150–170 l. of fluid passed daily out of the reticulo-rumen of a 530 kg cow. The calculated values in Table 4 suggest that 125–225 l. water entered the rumen, but make no allowance for absorption through the rumen wall.

SUMMARY

1. In cows with a permanent rumen fistula the rate of secretion of mixed saliva during eating was estimated by drying boluses of various foods collected at the cardia. The mean rate of secretion was 229 ml/min, which was two to four times greater than the rate of secretion of mixed saliva during rest.

2. The amount of saliva added to a given weight of food varied greatly with the different foods. The variations were due partly to differences in the rate of secretion of saliva with different foods, but mainly to differences in the rate at which the foods were eaten, the more fibrous foods being eaten more slowly than the less fibrous. These differences in the rate of eating were due primarily to differences in the size of the boluses, with smaller effects due to differences in the rate at which the boluses were swallowed.

3. Fluid squeezed from swallowed boluses of dairy cubes and two kinds of hay had a greater tonicity and higher concentration of certain inorganic ions than did mixed saliva secreted during rest. This finding suggested that ensalivation during mastication was effective in bringing soluble food constituents into solution.

4. Removal of the contents of the mouth during rumination suggested that up to 50% of the regurgitated solid material may escape re-mastication and be re-swallowed without further ensalivation. It is postulated that the increased flow of parotid saliva during rumination serves to wash the re-masticated digesta, from the space between cheek and teeth, into the oesophagus.

5. Tentative estimates suggest that the total daily secretion of mixed saliva in four cows varied from 98 to 190 l. with five different diets.

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