CXLIX. THE FASTING METABOLISM OF RUMINANTS

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IN a previous publication [Hutchinson & Morris, 1936], a short study was presented of the fasting catabolism of ruminants, together with a brief review of the more important studies up to that date. The present experiments were undertaken to obtain a more detailed analysis of the protein catabolism by means of systematic and complete analyses of both blood and urine. With the ruminant, most of the evidence in connexion with protein anabolism and catabolism has been obtained from experiments on feeding with normal or abnormal rations [Morris *et al.* 1936]. To understand completely the processes concerned, a study of the organism when living at the expense of its own tissues is essential. With water available the fasting animal obtains the energy necessary for the continuation of the life processes from the catabolism of its own store of carbohydrate, protein and fat.

The animals used in the present experiment were goats (2 lactating, 2 non-lactating), sheep (4 non-lactating) and cows (3 lactating). The animals fasted following a ration complete in all respects for their requirements. In the previous experiments [Hutchinson & Morris, 1936; Benedict & Ritzman, 1927] the animals were subjected to a period of low protein intake prior to starvation. In view of the statement by Aylward & Blackwood [1936] that demineralization of the osseous tissue takes place during fasting, the mineral (Ca and P) metabolism was studied in the case of the goats and sheep.

EXPERIMENTAL

During the pre- and post-fast periods collections of urine and faeces were made every 2nd day; during starvation daily collections and analyses were carried out. The lactating animals were milked twice daily, the evening and morning milk being bulked for analysis; with the goats the yield fell so low that only total N analyses could be made. So remarkable, with the goats, was the rise in N percentage in the milk that it was thought advisable, with the cows, to obtain a more detailed analysis of the nitrogenous products of the milk throughout the fast. A study was made of the casein, albumin, globulin and N.P.N. of the milk before, during and following the fast, though the results are not presented here.

Goat 2 died at the end of the 10-day fast, the urinary volume being abnormally high. Cow 1 suffered from "milk fever" on the 3rd day of the fast, but recovered within a few hours after udder inflation. From the results it is doubtful if the "milk fever", apart from 1 day, had any effect on the protein or mineral metabolism.

The methods used in the analyses were as follows:

Urine. Total N, Kjeldahl; urea and ammonia, Folin aeration; amino-acid N, Sørensen; creatinine, Jaffe; uric acid, Folin; purine base, Krüger-Schmidt; allantoin, Roy; Ca, McCrudden; P, Pemberton-Neumann.

Faeces. Total N, Kjeldahl; Ca, permanganate titration; P, Pemberton-Neumann.

Blood. Total N, Kjeldahl; serum albumin and globulin, Howe; amino-acid, Folin; N.P.N., micro-Kjeldahl; uric acid, Folin; Ca, Collip; P and phosphatase, Bodansky; sugar, Hagedorn-Jensen; Cl, Davies.

In the discussion of results the paper is divided into two parts:

1. Nitrogen metabolism:
 - (a) Urinary N partition.
 - (b) Faecal N excretion.
 - (c) Blood N partition.
2. Mineral metabolism:
 - (a) Ca excretion in urine and faeces.
 - (b) P excretion in urine and faeces.

DISCUSSION OF RESULTS

1. Nitrogen metabolism

(a) *Urinary N partition.* In the previous publication [Hutchinson & Morris, 1936] it was shown that, following a low N diet, the most marked effects on the urinary N partition were the increases in urea and creatine excretion. The ammonia output tended to fall off until the 8th day of fast when an increase above normal was noted. In all cases the urinary N excretion increased markedly during the fast, the true fasting catabolism being reached on the 4th to the 6th day, thus confirming the earlier work of Carpenter [1927]. The daily N excretion per kg. body-weight was found to be 0.088 to 0.13 g. for the cows, 0.13 g. for the goats and 0.16 g. for the sheep.

Table I shows the results in the present experiment. The total N excretion tends to decrease slightly as the fast continues. It must again be stressed that the fast followed a rich and complete diet for several months. The N excretion expressed as g. per kg. body-weight is as follows:

Goat				Sheep				Cow	
1	2	3	4	1	2	3	4	1	2
0.20	0.12	0.16	0.17	0.12	0.17	0.16	0.16	0.06	0.08

With the cows and sheep the results are slightly lower than in the previous experiment, whereas with the goats the results are higher. These differences would appear to be within the normal range and dependent on the age and state of nutrition of the animal prior to the fast.

Regarding the urinary partition, the urea, ammonia, amino-acid and hippuric acid excretions will be discussed first. With the goats, both the urea and ammonia N excretions when expressed as a percentage of the total N, increase as the fast progresses, whereas the hippuric acid N output decreases markedly. The amino-acid N excretion remains fairly normal. With the cows, only the urea increases, the ammonia, amino-acids and hippuric acid falling off markedly during the fast. With the sheep, both urea and ammonia increase, the amino-acids and hippuric acid decreasing. It will be seen that the percentage output follows closely the total output of these partition products. Comparing these results with the few reported in previous publications [Hutchinson & Morris, 1936; Carpenter, 1927], it will be noted that, on broad lines, both series of experiments are in agreement.

Table I. *Urinary partition of N*

Day of fast	Total N g.	Urea N g.	NH ₃ N mg.	Amino acid N mg.	Hippuric acid N mg.	Preformed creatinine mg.	Creatine mg.	Uric acid mg.	Purine base mg.	Allantoin g.
Goat 1										
Non-fast	4.84	3.39	160	110	530	310	100	70	150	0.89
1- 3	4.71	3.37	217	37	190	350	320	73	113	1.23
4- 6	3.68	2.74	290	90	53	340	63	60	237	0.66
7- 9	5.03	3.84	407	157	40	267	380	37	320	0.68
10	7.72	6.36	650	110	60	370	250	30	490	0.59
Post-fast	4.20	2.04	920	250	430	240	90	60	170	0.74
Goat 2										
Non-fast	4.50	3.14	150	100	510	360	130	60	140	0.89
1- 3	4.54	3.70	53	37	190	300	153	37	230	0.86
4- 6	3.57	2.56	130	57	50	373	277	40	200	0.62
7- 9	3.43	2.61	303	37	50	307	237	40	260	0.63
10	7.56	5.88	450	220	20	870	410	90	590	1.10
Goat 3 (lactating)										
Non-fast	6.18	3.50	190	40	1280	300	120	170	320	1.76
1- 4	7.69	5.01	263	165	1123	370	335	193	598	2.06
5- 8	5.86	4.83	245	155	133	305	230	63	345	0.50
9-12	4.12	2.95	548	83	20	298	123	45	295	0.51
Post-fast	5.28	2.79	390	230	820	260	90	120	230	1.67
Goat 4 (lactating)										
Non-fast	6.08	3.24	200	100	1100	280	150	150	500	1.55
1- 4	6.49	4.87	75	85	485	300	203	70	503	1.81
5- 8	5.42	4.26	150	95	193	348	243	78	595	0.73
9-12	5.31	4.01	278	78	75	340	333	80	520	0.79
Post-fast	4.60	1.73	480	230	860	200	60	80	240	1.80
Sheep 1										
1- 3	8.58	5.98	140	90	150	570	347	127	290	2.74
4- 5	6.49	4.65	285	50	70	690	135	150	415	1.70
6- 7	5.53	3.90	520	45	55	560	225	195	525	1.34
Post-fast	6.39	4.04	890	110	170	720	320	160	200	3.23
Sheep 2										
1- 3	7.34	4.87	153	233	187	640	513	113	310	2.61
4- 5	6.14	4.31	190	55	85	610	650	140	365	1.80
6- 7	7.86	5.80	415	115	135	845	350	270	560	1.85
Post-fast	5.34	2.58	820	130	130	760	440	180	180	2.93
Sheep 3										
1- 3	6.97	4.31	203	57	460	500	463	93	270	2.01
4- 5	8.64	6.25	640	80	80	840	430	60	360	1.22
6- 7	8.65	6.33	275	35	125	730	315	280	525	2.17
Post-fast	6.50	4.02	560	260	180	630	400	180	200	3.08
Sheep 4										
1- 3	8.65	6.58	177	87	173	580	260	160	410	2.83
4- 5	6.48	4.82	240	35	85	615	485	155	490	1.72
6- 7	5.97	4.53	375	40	10	580	265	185	610	1.40
Post-fast	4.50	2.50	230	170	70	560	350	180	200	2.36
Cow 1 (lactating)										
			g.	g.	g.	g.	g.	g.	g.	
Non-fast	39.32	13.96	9.48	4.04	2.18	3.56	0.74	0.71	1.83	11.57
1- 3	44.39	20.12	16.30	4.48	0.53	2.78	2.31	0.39	1.44	16.67
4- 6	37.26	7.77	20.99	3.57	0.25	2.57	1.81	0.22	1.11	7.99
7- 9	21.80	10.31	6.00	1.21	0.23	1.39	0.99	0.13	0.54	6.38
10-12	24.75	13.65	4.46	1.26	0.21	2.54	1.60	0.19	0.93	5.86
Post-fast	36.05	9.15	9.15	3.90	2.27	3.64	0.42	0.93	3.30	18.38
Cow 2 (lactating)										
Non-fast	37.28	14.30	11.95	3.85	2.61	4.08	0.74	0.71	1.83	11.57
1- 3	64.40	17.05	31.04	5.13	1.05	3.09	3.83	0.69	1.15	18.57
4- 6	36.15	19.49	7.51	2.90	1.13	4.02	2.47	0.30	0.81	4.78
7- 9	37.75	25.92	4.37	1.54	0.82	4.47	1.86	0.33	0.33	4.78
10-12	31.86	20.87	3.63	1.10	0.34	2.84	0.85	0.24	0.45	5.29
Post-fast	40.04	15.47	10.75	4.25	0.23	4.05	1.43	1.00	2.47	9.34

Regarding the creatinine and creatine metabolism (Table I), two points are evident, the normal or slightly subnormal value of the creatinine output and the large increase in the creatine excretion. The percentage creatinine N tends to increase slightly towards the 6th day of fast and then decreases. It is doubtful if the subnormal results are significant, since fairly large variations in the creatinine excretion are to be expected normally. Previous work on human subjects [Cathcart, 1921] has shown that there is a tendency towards a decreased output of both creatinine and creatine as fasting progresses. It is remarkable that only with the animal which died is there any marked increase in the creatinine output in the urine, corresponding with a marked increase in the urinary volume. From the complete correlation between urinary volume and creatinine excretion a hypothesis could be formulated regarding the formation of creatinine. A reversible enzyme reaction, such as

inhibited by the production of a relatively excessive amount of creatinine, would explain the constant excretion. The only condition which would permit of an excessive formation and excretion of creatinine would be one in which there was a marked diuresis with a consequent rapid and continuous flushing of the tissues, as in the case of goat 2. This would agree with the theory of Terroine & Champagne [1933] that creatinine metabolism is the final stage of some fundamental process.

It has been stated [Terroine & Mourot, 1931] that creatine is formed either from ingested protein, on feeding a protein-rich diet, or during starvation from body tissue. The former assertion, the increase in creatine excretion with an increased protein intake, we have not yet been able to confirm with ruminants [Hutchinson & Morris, 1936]; further work is, however, in progress to study this problem more fully. The increased creatine output during starvation has long been known, and it is reasonable to assume that this arises from active muscular catabolism. Whether the increase is merely the result of the protein catabolism or is due to the catabolism of some substance, a precursor of creatine but not connected directly with the true protein metabolism, is at present unknown.

The purine metabolism is shown in Tables I and II. As in the non-ruminants, the uric acid excretion decreases markedly both in total and percentage amount, with, as will be seen later, a marked increase in the blood level. The purine base compounds increase, both in total amount and when expressed as a percentage of the total N, with the goats and sheep, especially the non-lactating ones; with the cows a decrease is noted. With all the animals a decrease occurs in the allantoin excretion following an initial rise in the first 2 days. It is evident that the amount of the total N excreted as purine base metabolites has diminished considerably during starvation. The ruminant thus appears to reduce nuclear cell metabolism to a minimum in order to preserve the nucleoproteins which are essential for life processes. This fact was noted by Hutchinson & Morris [1936], who found that the percentage of total N in the urine present as undetermined N was reduced. They stated that "this fraction consists of the purine bodies, and it appears that the ruminant tends to retain these compounds by minimizing cellular metabolism during a fast". This agrees also with the results obtained with non-ruminants [Benedict, 1907; 1915; Cathcart, 1921]: It is, however, possible that a part of the purine bodies excreted arises by synthesis from non-purine material. It has been found that, whereas a fat-rich protein-poor diet decreases the purine output, a carbohydrate-rich diet causes a marked increase

Table II. *Percentage distribution of purine N*

	Days of fast													Post- fast
	Pre- fast	1	2	3	4	5	6	7	8	9	10	11	12	
Goat 1														
Uric acid	6	5	5	4	6	—	6	7	3	2	2	—	—	5
Purine base	12	5	10	10	19	—	35	32	32	28	44	—	—	16
Allantoin	82	90	85	86	75	—	59	61	65	70	54	—	—	79
Goat 2														
Uric acid	5	4	3	2	5	—	3	4	3	4	5	—	—	—
Purine base	12	16	17	25	22	—	22	23	30	28	32	—	—	—
Allantoin	83	80	80	73	73	—	75	73	67	68	63	—	—	—
Goat 3														
Uric acid	7	7	—	7	—	6	8	9	7	5	4	3	—	6
Purine base	12	11	—	14	—	36	35	39	18	32	24	32	—	10
Allantoin	81	82	—	79	—	58	57	52	75	63	72	65	—	84
Goat 4														
Uric acid	6	3	—	2	—	6	6	7	5	6	7	6	—	3
Purine base	22	21	—	18	—	44	23	35	43	30	35	30	—	11
Allantoin	72	76	—	80	—	50	71	58	52	64	58	64	—	86
Sheep 1														
Uric acid	—	1	2	7	6	6	10	8						
Purine base	—	6	14	8	19	16	15	32						
Allantoin	—	93	84	85	75	78	75	60						
Sheep 2														
Uric acid	—	3	2	7	7	6	10	9						
Purine base	—	10	10	8	19	11	19	21						
Allantoin	—	87	88	85	74	83	71	70						
Sheep 3														
Uric acid	—	4	1	7	—	4	8	10						
Purine base	—	11	17	6	—	21	15	20						
Allantoin	—	85	82	87	—	75	77	70						
Sheep 4														
Uric acid	—	3	2	7	6	6	8	7						
Purine base	—	8	16	13	19	23	18	33						
Allantoin	—	89	82	80	75	71	74	60						
Cow 1														
Uric acid	5	2	2	2	2	2	2	2	3	2	5	2	3	4
Purine base	12	6	19	10	9	16	10	8	9	6	19	13	15	14
Allantoin	83	92	89	88	89	82	88	90	88	92	76	85	82	82
Cow 2														
Uric acid	5	4	4	3	4	4	5	7	7	6	5	3	3	—
Purine base	12	6	4	6	16	14	11	5	6	4	8	5	7	—
Allantoin	83	90	92	91	80	82	84	88	87	90	87	92	90	—

[Cathcart, 1909; Graham & Poulton, 1913; Umeda, 1915]. Terroine & Mourot [1931] noted a direct correlation between the level of protein intake and the allantoin output in the urine. This may possibly be due to the presence in the protein molecule of amino-acids capable of being synthesized to purine compounds [Ackroyd & Hopkins, 1916; Lewis & Doisy, 1918]. Since, however, purine synthesis appears to be connected with carbohydrate metabolism, it can be safely concluded that during starvation, with a lack of carbohydrate, this synthesis can only take place to a very limited extent.

Examination of the distribution of the purine N (Table II) shows that the percentage distribution has been markedly altered throughout starvation. With

the goats the normal proportions of purine base, uric acid and allantoin are approximately 12 : 6 : 82, whereas in starvation they are 32 : 3 : 65; with the sheep the normal values 11 : 5 : 83 become 30 : 8 : 62. These results show a marked increase in purine base and as marked a decrease in allantoin. According to the commonly accepted theory of purine metabolism

there must have been a decrease both in the cellular oxidation of the nucleoproteins and in the oxidation of the purine base compounds formed during starvation by goats and sheep. With the cows, on the other hand, it is doubtful if the changes are significant. This is not the effect of lactation, since there is little difference between the lactating and non-lactating goats, but must be a species difference.

Although no difference is found between the lactating and non-lactating goats during starvation, it is interesting to compare the results obtained in the pre-fast period. The total amount of purine base derivatives is greater with the lactating animals. This increased cellular oxidation may be due both to the increased food intake and to a natural increase as the result of lactation.

It seems advisable at this stage to draw attention to the figures given by Hunter & Givens [1914], and now generally accepted, for the purine base distribution in the urine of goats, cows and sheep, and to compare them with the present values. It will be seen that, whereas Hunter & Givens found markedly different distributions for goats, sheep and cows, the present work indicates that there are, in fact, no significant differences in distribution.

	Goat		Sheep		Cow	
	H. and G.	Present work	H. and G.	Present work	H. and G.	Present work
Uric acid	7	6	16	5	7.3	5
Purine base	12	12	20	11	0.7	13
Allantoin	81	82	64	83	92	82

The sulphur excretion and the N : S ratio of the urine (Table III) show that a difference exists between the different species of ruminant. Whereas the goats and cows, towards the latter end of the fast, show a N : S ratio approximating closely to that of body tissue, the sheep show a ratio higher than that of body tissue, due to a marked retention of S. This may be due, at least in part, to the excessive requirements of S for wool production with sheep, and the attempt by the animals to retain as much body S as possible. The sheep were growing and this may also have had some effect on the ability of the animals to retain body S. It is possible, however, that the muscle or reserve protein catabolized in the course of the first 7 days' starvation is poor in S. Similar results were noted by Lewis [1916], who found a slight retention of S indicating the possibility of a retention of muscle tissue.

The N : P ratio (Table IV) falls rapidly as the fast progresses, from 350 to 17.5 with goat 1, to 6.5 with goat 2, to 21 with goat 3 and to 22 with goat 4. With the 4 sheep the ratio falls from 350 to about 18. With human beings [Cathcart, 1921] the ratio reaches a maximum after 12 to 14 days of about 6, the theoretical value for muscle being 6.6. Cathcart concludes that the bony tissue contributes materially to the P excretion in starvation, since the excretion of P in its relation to N is greater than the ratio of the two elements in muscle. Aylward & Blackwood [1936] came to the same conclusion with ruminants. They found that the N : P ratio towards the end of the fast was 11.6 instead of

Table III. *N-S ratios*

Day of fast	Goat				Sheep				Cow	
	1	2	3	4	1	2	3	4	1	2
Pre-fast	3.7	3.9	4.4	4.8	3.7	7.6	5.5	5.8	3.5	—
1	14.0	10.3	12.5	14.0	23.6	17.2	15.9	23.2	9.4	11.5
2	15.0	16.1	—	—	22.1	25.2	21.1	22.2	14.3	13.9
3	9.0	17.4	—	—	49.0	32.8	28.5	30.4	15.4	12.3
4	10.9	17.1	15.5	16.3	40.6	34.5	—	45.2	14.0	11.5
5	—	—	16.1	14.2	31.5	24.2	23.4	33.0	17.8	10.6
6	10.6	15.6	14.3	17.4	33.7	21.1	23.4	33.6	14.3	13.9
7	9.6	16.2	15.5	16.2	30.0	20.8	18.3	29.2	15.1	15.4
8	12.2	15.3	16.1	15.3	—	—	—	—	14.2	18.8
9	13.6	13.9	14.9	16.5	—	—	—	—	16.6	19.1
10	14.4	14.0	17.2	13.3	—	—	—	—	12.9	17.6
11	—	—	15.4	16.2	—	—	—	—	14.9	18.1
12	—	—	15.7	16.3	—	—	—	—	11.6	16.9
Post-fast	4.4	—	—	—	—	—	—	—	—	—

Table IV. *N-P ratios*

Day of fast	Goat				Sheep			
	1	2	3	4	1	2	3	4
Pre-fast	345	350	258	320	345	236	255	551
1	—	—	—	—	360	320	248	287
2	87.7	63.5	91	95	255	229	310	300
3	—	—	—	—	430	126	273	170
4	—	—	—	—	105	40	542	52
5	11.0	8.4	56	51	19.2	24	—	38
6	—	—	—	—	19.5	15	29	24
7	17.5	6.5	22	23	16.9	15	18	20
8	—	—	—	—	16.0	17	24	15
9	—	—	21	22	—	—	—	—

17.4, and state that bone demineralization must take place to account for the decrease in the ratio. In the present experiment no such assumption is necessary, since the P arising from the catabolism of muscle can account for all the urinary P excreted. From the results with goat 2, which died at the end of the fast, it would appear, more especially from the N : P and N : S ratios, that the last 3 days of the fast correspond to the immediate premortal stage in the life of the animal. With goat 1 the ratio of N : P fell markedly from the 4th to the 7th day of the fast, as did also the N : S ratios. This abnormal output of P and S cannot at present be explained, but is obviously the result of excessive catabolism of some tissue rich in P and S.

It is doubtful if the daily variations in the N : P and N : S ratios are significant; it may be advisable to average the ratios from the 4th day of fasting. In the present experiment this would still yield ratios of 17 or more, which correspond to those found in the experiments of Aylward & Blackwood [1936].

(b) *Faecal N excretion.* In a previous publication [Hutchinson & Morris, 1936] the constant fraction of the metabolic faecal N of cows was determined. The average value was 7 g. daily. In the present investigation values have been obtained for goats, cows and sheep (Table V). From the 4th day the faecal N remained fairly constant, except with the sheep. The average values of the daily faecal N output are, from the 4th to the last day of fast,

Goat				Sheep				Cow	
1	2	3	4	1	2	3	4	1	2
0.39	0.44	0.35	0.50	0.49	0.49	0.88	0.68	6.7	6.6

Table V. *Faecal N output, g.*

Day of fast	Goat				Sheep				Cow	
	1	2	3	4	1	2	3	4	1	2
Pre-fast	4.02	2.95	5.33	5.59	7.13	8.82	8.03	6.79	93.27	96.40
1	2.08	2.20	—	—	1.63	3.26	3.26	1.69	52.90	44.50
2	1.45	0.85	6.20	5.98	0.72	1.00	0.70	0.57	33.60	27.50
3	1.04	0.64	—	—	1.07	0.67	0.97	0.96	10.58	16.30
4	1.33	1.09	2.90	2.24	0.44	0.18	—	0.32	—	15.37
5	—	—	0.78	0.42	0.61	0.65	—	0.95	19.24	16.68
6	—	0.76	1.00	0.68	0.56	0.47	1.97	0.91	5.88	11.03
7	0.37	—	0.58	0.60	0.34	—	1.62	0.36	11.74	12.60
8	—	—	0.28	0.75	—	—	—	—	—	8.11
9	0.66	0.60	0.26	0.50	—	—	—	—	5.07	6.28
10	—	—	0.28	0.24	—	—	—	—	2.96	5.94
11	—	—	0.38	0.45	—	—	—	—	—	6.18
12	—	—	0.32	0.33	—	—	—	—	11.85	—
Post-fast	3.42	—	5.58	5.08	—	—	—	—	62.70	64.28

The average works out at 0.42 g. for goats, 0.64 g. for sheep and 6.5 g. for cows. The value for the sheep is higher than would be expected, but this is probably the result of the short fast (7 days) as compared with 10 and 12 days for the goats and cows. It will be seen that the results for the cows agree with those previously recorded. From work on a fasting dog, Voit [1894] noted that the ordinary starvation faeces cannot consist of the total of the excretions from the body into the alimentary tract, but rather represent their unabsorbed remainder. In the human subject, Benedict [1915] found that during a fast of 31 days no faeces were excreted at all.

(c) *Blood N partition.* The blood analyses (Table VI) show an increase in both the protein and non-protein fractions. The apparent increase in total protein, although in some cases slight, is nevertheless definite and significant. It is, however, probably not the result of a true increase but rather due to a slight dehydration of the blood. This is borne out by an examination of the change occurring in the corpuscular volume during starvation. A marked increase is noted in the case of the cows (Table VII). In the dog and rat no such increase in corpuscular volume was found [Robertson, 1912-13].

Analysis of the protein partition shows that both albumin and globulin increase to a varying degree. In both goats and sheep the globulin increases to more than 50 % of the total protein, whereas in the cow the increase is very much smaller, the albumin increasing to a greater extent. Lewinski [1903] found an increase in the globulin fraction in a fasting dog but no change in the albumin. Robertson [1912-13] found that in the dog and rat starvation led to an increase in the globulins, whereas in the rabbit, ox and horse the albumins increased.

The increase in urea and amino-acid N may also be explained by dehydration. On the other hand, the increase in the undetermined fraction of the N.P.N. cannot be due to dehydration. It is this fraction, with the goats and cows, which causes the increase in the N.P.N. The nature of this fraction is at present unknown. It may be noted that, with the sheep, the undetermined N is higher in the post-fast period than during starvation. This may possibly be the result of the low P ration on which the animals subsisted both before and after the fast.

With all animals the uric acid increases markedly. Similar results have been recorded with human beings [Cathcart, 1921], in whom uric acid is the chief end product of the purine catabolism.

The blood sugar and Cl results are also included (Table VII). With cow 1, at the height of the "milk fever", the blood sugar rose markedly. During the

Table VI. *Blood N partition*

Period	Total protein g.	Albumin g.	Globulin g.	N.P.N. mg.	Urea N mg.	Amino- acid N mg.	Uric acid mg.	Undeter- mined N.P.N. mg.
Goat 1								
Pre-fast	6.00	3.40	2.60	27.00	13.04	5.84	—	8.12
Fast	6.76	3.72	3.04	35.80	21.00	6.28	—	8.52
Post-fast	6.09	3.24	2.75	31.00	14.88	5.80	—	10.32
Goat 2								
Pre-fast	6.43	3.32	3.11	27.00	16.62	6.02	—	4.36
Fast	7.13	3.58	3.55	37.60	25.02	5.98	—	6.60
Goat 3								
Pre-fast	5.90	3.08	2.82	21.80	14.82	5.02	—	1.96
Fast	6.54	3.17	3.37	28.20	18.94	5.88	—	3.38
Post-fast	6.08	3.12	2.96	22.22	16.42	5.56	—	0.24
Goat 4								
Pre-fast	6.69	3.38	3.31	19.60	11.68	4.84	—	3.08
Fast	7.27	3.42	3.85	23.60	16.04	5.02	—	2.54
Post-fast	6.35	3.26	3.09	17.70	12.84	4.78	—	0.08
Sheep 1								
Fast	6.14	3.08	3.06	32.20	22.02	7.44	0.08	2.74
Post-fast	6.08	3.00	3.08	27.00	18.40	5.48	0.07	3.12
Sheep 2								
Fast	6.66	3.28	3.38	34.70	24.00	7.76	0.12	2.94
Post-fast	6.22	3.30	2.92	31.00	19.20	5.14	0.09	6.66
Sheep 3								
Fast	6.46	3.19	3.27	34.10	23.66	7.88	0.08	2.56
Post-fast	6.25	3.21	3.04	32.00	19.70	5.64	0.07	6.66
Sheep 4								
Fast	6.58	3.22	3.36	35.20	24.02	7.38	0.10	3.80
Post-fast	5.93	3.10	2.83	32.00	18.80	5.66	0.07	7.54
Cow 1								
Pre-fast	—	4.13	—	15.68	7.94	6.69	—	1.05
	7.89	4.19	3.70	19.60	8.00	6.44	—	5.16
	9.44*	5.47	3.97	24.50	8.92	7.07	—	8.51
Fast	8.22	4.96	3.26	24.10	11.33	6.30	—	6.47
	8.17	4.86	3.31	32.20	9.70	7.56	0.12	14.94
	8.21	4.84	3.37	24.00	13.00	7.21	—	3.19
Post-fast	7.61	4.05	3.56	23.80	9.50	6.65	—	7.65
	8.06	4.74	3.32	17.80	10.44	6.88	—	0.48
Cow 2								
Pre-fast	7.50	4.34	3.16	17.68	8.24	7.07	—	2.37
	7.60	4.62	2.98	19.20	8.00	6.37	—	4.83
	7.93	4.78	3.15	19.80	9.02	6.44	—	4.34
Fast	8.06	5.12	2.94	22.10	9.00	6.93	0.05	6.17
	8.50	5.21	3.29	28.70	10.28	7.42	0.05	11.00
	8.35	5.02	3.33	31.90	11.73	7.46	0.14	12.71
Post-fast	7.21	4.48	2.73	22.40	10.70	6.64	—	5.06
	7.93	4.78	3.15	17.91	11.00	6.86	—	0.05

* Milk fever.

Table VII. *Blood analyses*

Period	Corpus- cular vol. %.	Ca mg./ 100 ml.	Inorganic P mg./ 100 ml.	Phos- phatase units	Cl mg./100 ml.		Sugar mg./100 ml.	
					Blood	Plasma	Blood	Plasma
Goat 1								
Pre-fast	—	9.1	5.4	8.5				
Fast	—	8.2	6.9	7.6				
Post-fast	—	9.2	4.8	8.6				
Goat 2								
Pre-fast	—	8.5	6.4	7.7				
Fast	—	8.0	12.0	3.5				
Goat 3								
Pre-fast	—	9.8	5.5	6.7				
Fast	—	8.1	7.2	4.2				
Post-fast	—	9.7	6.0	5.7				
Goat 4								
Pre-fast	—	10.4	4.9	6.9				
Fast	—	8.6	6.9	4.8				
Post-fast	—	9.4	5.9	7.0				
Sheep 1								
Fast	—	9.9	9.2	5.0				
Post-fast	—	13.4	2.7	12.8				
Sheep 2								
Fast	—	10.7	10.0	5.3				
Post-fast	—	12.2	3.1	11.7				
Sheep 3								
Fast	—	10.0	11.0	4.7				
Post-fast	—	13.6	2.2	11.4				
Sheep 4								
Fast	—	10.5	9.7	5.5				
Post-fast	—	14.1	2.4	13.0				
Cow 1								
Pre-fast	33.3	8.4	—	—	303	359	41.8	53.6
	34.0	—	—	—	298	360	39.1	54.2
	33.3	8.6	5.8	5.0	306	355	46.7	53.8
Fast	43.0*	5.8	4.3	3.9	271	343	147.5	208.0
	40.0	7.9	7.4	5.7	283	338	52.2	65.7
	38.0	7.5	5.2	5.5	282	334	56.4	68.1
	36.0	7.8	5.4	6.0	272	323	57.2	71.6
Post-fast	29.0	8.6	5.3	4.7	305	357	67.4	78.6
	30.0	9.8	4.3	5.4	301	360	55.2	58.7
	31.0	—	—	—	301	357	52.7	67.7
Cow 2								
Pre-fast	33.3	10.2	5.7	4.5	305	363	46.8	55.8
	32.5	10.6	5.1	4.7	306	368	44.5	53.6
	31.1	10.5	5.0	5.0	279	346	40.0	48.3
Fast	40.0	9.8	5.9	3.0	275	347	47.3	63.2
	41.0	10.2	6.5	4.1	267	337	48.7	67.8
	42.0	8.1	7.2	3.2	267	323	51.2†	71.5
Post-fast	33.3	10.6	4.6	4.8	296	365	45.0	58.4
	32.0	10.8	4.6	4.2	307	375	66.7†	87.0
	35.0	—	—	—	287	352	51.6	64.3

* Milk fever.

† Great difficulty in obtaining blood sample.

course of normal starvation, however, there may be a tendency towards a rise in blood sugar, but the significance of the results is doubtful. The effect of excitement on the blood sugar level has long been known and is well exemplified with cow 2, where an increase was noted when blood samples were obtained only with great difficulty. Aylward & Blackwood [1936] found no change in the blood sugar level of fasting cows. In non-ruminants glucose is present in the blood up to the last day of life, being produced, probably, from the metabolized protein [Lusk, 1931].

The Cl content of both whole blood and plasma decreases slightly during starvation. In non-ruminants plasma Cl decreases during starvation [Gamble *et al.* 1923; Goto, 1923; Weeks *et al.* 1923], the reduction being due, in part, to migration of Cl from plasma to cells as a result of fasting acidosis [Peters & Van Slyke, 1931]. With ruminants no change was noted in the corpuscular concentration of Cl.

2. Mineral metabolism

(a) *Ca excretion in urine and faeces.* With the progress of the fast the urinary Ca decreased markedly (Table VIII), and, with the sheep, almost disappeared. The faecal excretion of Ca fell steadily throughout the fast. With the goats the percentage faecal Ca in the dry faeces rose during the fast, although the total output fell, whereas with the sheep both the percentage and total output decreased. During the pre-fast period all the animals were in positive Ca balance.

(b) *P excretion in urine and faeces.* With the goats and sheep the urinary P rose rapidly immediately starvation began (Table VIII). With cows Aylward & Blackwood [1936] found that the pre-fast level was maintained for the first 4 days of starvation, a rise in urinary P excretion beginning on the 5th day. It has already been shown that the urinary P during starvation in ruminants can be accounted for by the protein catabolized. The faecal P output, on the other hand, fell markedly, at times to an amazingly low figure (sheep 1, 2 and 4). With both goat 1 and sheep 3 the increase in P excretion towards the end of the fast may be due, in part, to the voiding of very soft faeces in large amounts. It will be seen (Table V) that the faecal N excretion was extremely high on those days. During those days the percentage of P in the dry faeces, which had been falling markedly, rose to a very high level. With the other animals the percentage fell steadily throughout starvation. In the pre-fast period the sheep were in negative P balance, owing to a P deficiency in the diet. With cows, Aylward & Blackwood [1936] found that there was a marked increase in the P percentage in the faeces during starvation.

In the ruminant the contents of the digestive tract are never completely removed even after 8 days' starvation [Grouven, 1864]. Thus we have a state of minimum food intake rather than true starvation. In accounting for the Ca and P in the faeces this fact must be considered. Whereas in the non-ruminant during starvation any faecal Ca and P must be endogenous in origin, it is reasonable, with ruminants, to assume that a part at least will come from the food residues. This view finds support in the constancy of the Ca : P ratio in the pre-fasting and fasting faeces of the goats and sheep (Table IX). Further evidence on this point can be found in the results of Turner *et al.* [1934]. They found that in ruminants considerable amounts of Ca and P may be retained as insoluble compounds in the intestinal tract for several weeks.

In view of these facts it seems that the assumption made by Aylward & Blackwood [1936], that the faecal P and Ca are entirely endogenous in origin, must be fallacious. The possibility of a part of the Ca and P excretion being

Table VIII. *Ca and P output, g.*

Day of fast	Goat 1				Goat 2				Goat 3				Goat 4			
	Faeces		Urine		Faeces		Urine		Faeces		Urine		Faeces		Urine	
	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P
Pre-fast	1.94	1.57	0.044	0.046	1.46	1.18	0.068	—	2.96	2.08	0.176	0.024	3.37	2.49	0.182	0.019
1	1.01	1.46	—	—	1.18	1.06	—	—	3.39	2.50	—	—	4.47	3.27	—	—
2	0.86	0.62	0.024	0.402	0.45	0.36	0.072	0.244	—	—	—	—	—	—	0.202	0.274
3	0.62	0.34	—	—	0.42	0.19	—	—	—	—	—	—	—	—	—	—
4	0.57	0.32	—	—	0.66	0.24	—	—	0.93	0.70	0.348	0.337	2.10	1.35	—	—
5	—	—	0.020	1.280	—	—	0.030	1.780	—	—	—	—	0.35	0.26	—	—
6	—	—	—	—	0.47	0.10	—	—	0.44	0.28	0.072	0.324	0.42	0.29	0.088	0.308
7	0.23	0.14	—	—	—	—	—	—	0.39	0.27	—	—	0.28	0.21	—	—
8	—	—	—	—	—	—	—	—	0.64	0.44	0.018	0.507	—	—	—	—
9	0.37	0.53	0.012	0.130	0.39	0.10	0.018	1.940	0.48	0.32	—	—	0.18	0.14	0.017	0.682
10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	0.30	0.23	0.008	0.489	0.18	0.14	0.024	0.506
12	—	—	—	—	—	—	—	—	—	—	—	—	0.19	0.15	—	—
Post-fast	1.92	1.36	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Day of fast	Sheep 1				Sheep 2				Sheep 3				Sheep 4			
	Faeces		Urine		Faeces		Urine		Faeces		Urine		Faeces		Urine	
	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P	Ca	P
Pre-fast	3.05	1.05	0.097	0.009	3.18	1.04	0.069	0.015	2.82	1.35	0.086	0.017	2.60	1.02	0.083	0.011
1	1.26	0.43	0.027	0.040	2.75	0.99	0.058	0.028	2.01	0.80	0.044	0.021	—	—	0.127	0.028
2	0.66	0.13	0.016	0.018	0.89	0.23	0.048	0.076	0.34	0.13	0.185	0.034	0.46	0.15	0.074	0.030
3	1.02	0.25	0.012	0.084	0.61	0.18	0.031	0.142	0.66	0.25	0.077	0.010	0.79	0.29	0.085	0.240
4	0.43	0.12	0.008	0.376	0.26	0.07	0.022	0.332	—	—	—	—	0.28	0.11	0.024	0.201
5	0.64	0.17	0.008	0.288	0.60	0.18	0.006	0.280	—	—	0.042	0.304	0.79	0.33	0.014	0.316
6	0.56	0.18	0.010	0.301	0.41	0.12	0.020	0.392	0.66	0.29	0.00	0.622	0.73	0.30	0.014	0.316
7	0.32	0.10	0.008	0.382	—	—	0.006	0.508	1.00	0.42	0.010	0.233	0.27	0.10	0.008	0.407

Table IX. *Ca : P ratios in faeces of goats and sheep*

	Ca : P		
	Pre-fast	Fast	Post-fast
Goat 1	1.24	1.30	1.41
2	1.24	3.25	—
3	1.42	1.46	—
4	1.36	1.33	—
Sheep 1	2.90	3.06	—
2	3.05	2.85	—
3	2.45	2.44	—
4	2.55	2.43	—

endogenous in origin cannot be entirely ruled out. A small part probably arises from the various intestinal secretions. Also there is a marked increase in the inorganic P content of the faeces during starvation, as shown by the following figures representing mg./100 g.:

	Cow 1	Cow 2	Cow 3
Pre-fast	40	41	41
End of fast	326	139	169

The high serum P (Table VII) may necessitate the formation of a colloidal Ca-P compound, to which the kidney is impermeable, which is excreted into the gut and faeces. If, however, there is any marked catabolism of osseous tissue, the excretion of Ca and P from this source must be through the faeces, since the urinary Ca during starvation is negligible, and since it has already been shown that the urinary P can be accounted for by the muscular catabolism. Although the fact that the Ca : P ratio in faeces is roughly constant throughout is in accordance with the idea that bone is broken down and both the Ca and P are excreted by way of the faeces, this would materially alter the Ca : P ratio of the faeces, giving an increase with the goats and a decrease with the sheep, since the ratio in bone is approximately 2 : 1. Aylward & Blackwood [1936] did find a difference in the ratio of Ca : P between the pre-fast and the starvation faeces.

SUMMARY

1. A complete study has been made of the fasting catabolism of ruminants: cows, goats and sheep.
2. The daily urinary N excretion per kg. body-weight was 0.06–0.08 g. for cows, 0.12–0.20 g. for goats and 0.12–0.16 g. for sheep.
3. The daily faecal N output was 6.6 g. for cows, 0.35–0.50 g. for goats and 0.49–0.80 g. for sheep.
4. The preformed creatinine tended to diminish slightly during the fast, whereas the creatine rose markedly.
5. The purine metabolism showed a fall in the output of uric acid and allantoin but an increase in that of purine base.
6. Blood analyses showed an increase in both the protein and non-protein nitrogen fractions. Whereas the increase in protein could be explained by a slight dehydration of the blood, the increase in the N.P.N., due chiefly to an increase in the undetermined fraction, could not be explained. A marked increase in blood uric acid was noted.
7. It was also shown that even in a 12-day fast there appeared to be no catabolism of osseous tissue with ruminants.

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