Problems in estimating the extent of coprophagy in the rat

BY GLADYS FAJARDO* AND H. HÖRNICKE†

Universität Hohenheim, Institut für Zoophysiologie, D 7000 Stuttgart 70, West Germany

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The quantity of re-ingested faeces was calculated by comparing faecal dry matter of unrestricted rats and coprophagy-restricted rats after correcting for differences in food intake. Due to high day-to-day variations of produced and re-ingested faeces it was not possible to calculate precisely the extent of coprophagy of an individual rat at a particular day with this difference method. Reliable quantitative estimates require at least two rats and a collection period of 7 d. When fed on a nutritionally complete diet, rats re-ingested 0–11 % of their faeces. When fed on low-protein diets (66 g egg albumin/kg) or diets diluted with 200 g cellulose/kg, coprophagy was not significantly increased. A high re-ingestion rate (6–25 %) was observed with thiamin and pantothenic acid deficiencies. After re-ingestion of faeces had been prevented for 1 week, the amount of faeces re-ingested during the subsequent week without tail-cups was increased twofold. It is concluded that rats are able to regulate the amount of faeces eaten precisely according to their requirements.

Coprophagy: Rat

Coprophagy, i.e. the re-ingestion of faeces, is of nutritional importance (Barnes, 1962; Giovanetti, 1982). It occurs in many rodent species (Björnhag & Sjöblom, 1977; Kenagy & Hoyt, 1980), but also in many other taxonomically unrelated mammals (Hörnicke & Björnhag, 1980; Chilcott, 1984) and even in birds (Steffens & Menke, 1964). The consumption of faeces improves the supply of B-vitamins and of vitamin K (Schulze & Haenel, 1969). Under certain conditions it also has a positive effect on nitrogen balance by making available bacterial protein synthesized in the hindgut (Stillings & Hackler, 1966; Giovanetti *et al.* 1970).

Re-ingestion was observed and studied in the laboratory rat several decades ago (Osborne & Mendel, 1911). Its importance for accurate methodology and interpretation of nutrition experiments and balance trials has been emphasized (Giovanetti, 1982; Neale, 1982). Re-ingestion prolongs the retention time of drugs and other substances administered, and thus favours absorption (Thomas & Roe, 1974). Prevention of coprophagy, on the other hand, accelerates the development of deficiency states during the ingestion of diets deficient in vitamins, protein (Hötzel & Barnes, 1966) or minerals (Tadayyon & Lutwak, 1969).

In spite of the practical importance of such information, accurate values relating to the extent of coprophagy under different conditions are scarce. According to Barnes (1962), rats eat 35–50 % of their faeces. This percentage can increase up to 100 % in severe vitamin deficiency. It thus appears that animals are able to regulate the amount of faeces consumed according to their nutritional state. This raises the question of whether coprophagy ceases altogether when a complete, nutritionally balanced diet is consumed.

Prevention of coprophagy is assumed to alter the nutritional state of coprophagic animals. Consequently all methods of preventing coprophagy can be expected to modify

* Present address: Depto Biología, Universidad Nacional, A. aéreo 23 227, Bogotá, Colombia.
† For reprints.

Table 1. *Composition of the diets (g/kg)*

(1)	Control diet*	
	Glucose monohydrate	516·5
	Egg albumin†	265·0
	Maize oil	80·0
	Cellulose powder	60·0
	Mineral mixture	56·4
	Vitamin mixture	20·0
	Trace element mixture	2·0
(2)	Test diets, obtained by modification of the control diet	
	Low-protein	Egg albumin lowered to 66·3 g/kg in exchange for glucose
	High-cellulose	Cellulose content raised to 200 g/kg at the expense of glucose
	Thiamin-deficient	Omission of thiamin from the vitamin mixture
	Pantothenate-deficient	Omission of calcium pantothenate from the vitamin mixture

* For details see Scheuermann & Lantzsch (1982*a*).
† Containing no thiamin, but 10·5 mg pantothenate/kg dry matter.

the process to be studied. The present study investigated the effects of different approaches to the measurement of the extent of coprophagy. We attempted to correct for these effects in order to estimate more precisely the re-ingestion rate during different feeding regimens. The ability of the animals to regulate the extent of coprophagy in protein and vitamin deficiencies and during the addition of cellulose to the diet was also studied.

METHODS

Animals

Male Sprague–Dawley SIV-50 rats (Ivanovas, Kieslegg) with initial weights of about 100 g were used. They were kept in a room with 12 h light–12 h dark; room temperature was about 20°, relative humidity about 50%. During adaptation to the diet and during the experiments the rats were kept in Macrolon III cages divided longitudinally by a plastic wall. Each animal had a compartment of 350 × 120 × 150 mm with a metal grid or plastic-bar floor. A feeder of the type described by Scheuermann & Lantzsch (1982*a*) reduced spillage and permitted the total collection of all feed not eaten. Access to food was over a grid of plastic bars; food particles found under the grids were returned to the food-cup before weighing. To prevent re-ingestion of faeces, tail-cups as developed by Scheuermann & Lantzsch (1982*b*) were used. They were made of Plexiglass and consisted of two halves which could be hooked together. They were fastened to the tail by adhesive tape and emptied at least every 8 h.

Diets

Synthetic diets with varying contents of cellulose and protein were prepared (Table 1). The control diet with (g/kg) 265 protein and 60 cellulose was found to give optimal growth in rats of the same strain and age (Scheuermann & Lantzsch, 1982*a*).

Calculations

Model 1

$$\text{FR (g)} = \text{FP} - \text{FC},$$

$$\text{FR (\%)} = \frac{\text{FP} - \text{FC}}{\text{FP}} \times 100,$$

where FR (g) is the amount of faeces re-ingested, FP and FC are the amounts of faeces collected when coprophagy was prevented and permitted respectively, and FR (%) is the percentage of the produced faeces re-ingested. This model gives reliable results only when food intake and digestibility during the unrestricted-coprophagy (control) and restricted-coprophagy (prevented) periods are the same. This is rarely the case. Food intake changes with time in growing animals. It may also change due to the presence of the tail-cup. The animals are then either irritated or deprived and eat less, or they compensate for the withdrawal of faeces by eating more food.

For model 1A, each animal was its own control, i.e. periods with and without tail-cups were compared. For model 1B, a group of animals with tail-cups was compared with another group without cups, but kept under otherwise identical conditions.

Model 2. This model corrects for differences of feed intake between control rats and prevented rats.

$$\text{FR (g)} = a \times (\text{FP} - \text{FC}),$$

$$\text{FR (\%)} = \frac{a \times (\text{FP} - \text{FC})}{a \times \text{FP}} \times 100 = 100\left(1 - \frac{(\text{FC} \times \text{IP})}{(\text{FP} \times \text{IC})}\right),$$

where a is food intake during control periods without cups (IC) divided by food intake during prevention of coprophagy (IP). Faecal excretion during the prevention of coprophagy is thus corrected for the food intake of the control rats, assuming proportionality between food intake and faeces excretion. Like model 1, model 2 can be applied in two different ways: model 2A, sequential studies in the same animals; model 2B, simultaneous measurements in different animals.

Experimental design (Fig. 1)

The 7-week study was designed to investigate the long-term effects of complete and of deficient diets on coprophagy, as well as the effects of alternating periods with and without tail-cups on food consumption, growth and coprophagic behaviour. It was conducted as two experiments with three diets each. Expt 1: group A, protein-deficient diet (66·3 g albumin/kg); group B, 200 g cellulose/kg diet; group C, control diet. Expt 2: group D, thiamin-deficient diet; group E, pantothenate-deficient diet; group F, control diet.

There were six rats in each group. They were allotted to three subgroups: *a*, two animals had no tail-cups and could always eat faeces; *b*, two animals had tail-cups every second week beginning with week 1; *c*, two animals had tail-cups throughout the experiment. In Expt 2 new rats were used and the design was modified in the following way: *a*, two animals had no tail-cups; *b*, two animals had tail-cups every second week beginning with the first week; *c*, two animals had tail-cups every second week beginning with the second week. Thus when two animals in subgroups *b* and *c* had cups, the other two could eat their faeces.

These arrangements allowed the calculation of the extent of coprophagy in different ways and under different conditions (Fig. 1): coprophagy of subgroup *a*, which was not hindered from eating faeces and served as a control, could be calculated by comparison with either

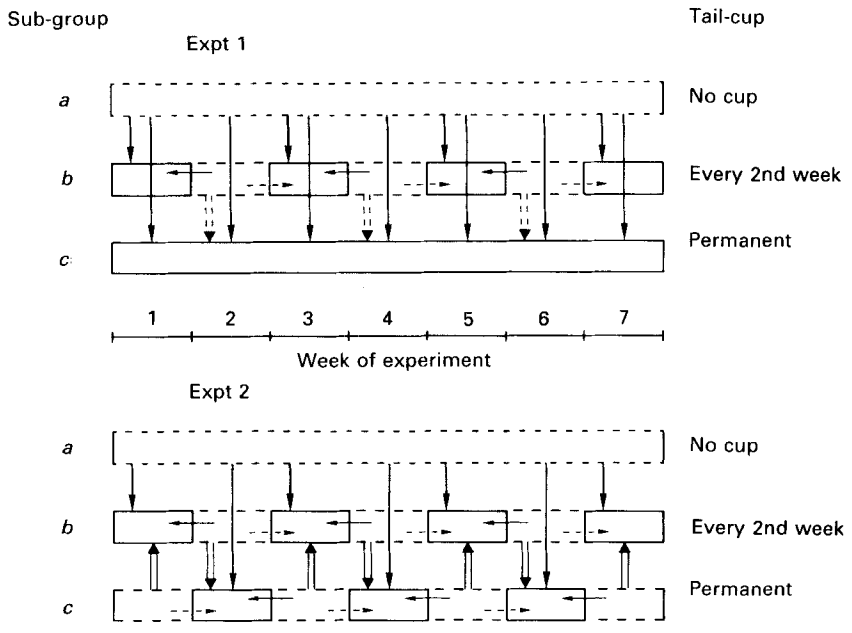

Fig. 1. Design of Expts 1 and 2 with the different methods for calculating the extent of coprophagy.
Model 2A: ←, comparison with previous week; →, comparison with subsequent week.
Model 2B: ⇓, rats permanently without tail-cups compared with rats periodically with tail-cups; ⇓, rats permanently without tail-cups compared with rats continuously with tail-cups; ⇓, comparison of the temporarily unprevented rats with temporarily or permanently prevented rats.

the periodically prevented rats during the period with cups, or (in Expt 1 only) with the permanently prevented rats of subgroup *c* (models 1B and 2B). Coprophagy of the intermittently prevented rats could be calculated by comparison with the permanently prevented animals (Expt 1 only) or (in Expt 2) with their temporarily prevented group-mates (models 1B or 2B), or by using their own results during the previous or subsequent week (models 1A or 2A).

RESULTS

Food consumption and weight gain (Table 2)

The rats on the balanced diet and without a tail-cup had the highest food consumption and the best weight gain. Prevention of coprophagy every second week reduced food intake by 18% and lessened weight gain in the same proportion. The rats with permanent tail-cups also ate 19% less, but their weight gain was greatly reduced (−35%), indicating a significantly reduced food utilization. The low-protein diet reduced food consumption, food utilization and weight gain. The effects of periodic prevention of coprophagy on food utilization could be fully compensated by a higher food consumption. Permanent prevention of coprophagy had the same effects as in the control group. The rats on the diet supplemented with cellulose consumed less and had a lower weight gain than the controls. However, with this diet the negative effects of a tail-cup could be fully compensated by a higher food consumption and no reduction in weight gain occurred. The thiamin-deficient rats lost appetite at the beginning of the second week. This resulted in weight loss after 14 d. As a consequence, the overall food intake for 7 weeks was only 43% of that of the controls and there was almost no weight gain. No significant effects of prevention of

Table 2. *Weight gain and food consumption of rats with and without tail-cups, fed on different diets*†

(Mean values and standard deviations)

Diet	Prevention of coprophagy	No. of rats	Wt gain in 7 weeks (g)		Food consumption (g/d)			Food consumption (g/g wt gain)
			Mean	%	Mean	SD	%	Mean
Control	None	4	217	100	20·56	2·55	100	4·6
	Periodically	6	175	81	16·84	1·78	82***	4·7
	Permanent	2	142	65	16·64	2·62	81***	5·7
62·5 g protein/kg	None	2	108	100	15·22	2·32	100	6·9
	Periodically	2	106	98	16·49	2·36	108	7·6
	Permanent	2	70	65	14·15	1·47	93	9·9
200 g cellulose/kg	None	2	150	100	16·22	1·69	100	5·3
	Periodically	2	150	100	18·45	2·95	114	6·0
	Permanent	2	154	100	18·59	2·90	115*	5·9
No thiamin	None	2	15	100	8·94	4·39	100	28·4
	Periodically	4	39	255	9·32	4·60	104	11·7
No pantothenate	None	2	205	100	17·92	1·77	100	4·3
	Periodically	4	197	91	16·51	3·02	92	4·1

%, Percentage of the 'no prevention of coprophagy' measurement, for each diet group considered separately.
Mean values were significantly different from '100%' values: * $P < 0{\cdot}05$, *** $P < 0{\cdot}001$.

† For details of diets and procedures, see pp. 552–554 and Table 1.

coprophagy could be observed. The pantothenate-deficient diet was well consumed and utilized; the gain was almost the same as with the balanced diet. Periodic prevention of coprophagy reduced growth in proportion to food intake.

Variability of food consumption and faeces production

The quantity of faeces re-ingested daily varied considerably among individual rats. In order to analyse the source of this high variability the coefficients of variation (CV) of food consumption and faeces excretion during the consumption of the control diet were calculated (Table 3). In animals with tail-cups food consumption was slightly reduced (−5%), but its variation was small and similar to that of rats without tail-cups (CV 9–16%). The amount of faeces excreted by these rats had a higher variability (CV 17–26%) than the amount of food consumed. In rats without tail-cups, access to faeces increased the variability further to 26–41%. This indicated: (1) the daily amount of faeces varied more than food intake, presumably due to variations in gastrointestinal passage and fill, (2) the amounts of faeces eaten varied from day to day. It is therefore not possible to calculate accurately the daily extent of re-ingestion on the basis of faeces collected from single animals. To reduce variability, we subsequently calculated rates of coprophagy by using pooled values of food and faeces from at least two animals or values from 7 d, or both.

Coprophagy of rats on the control diet

The results from different calculations for the quantity of re-ingested faeces are shown in Table 4.

(a) *Rats permanently without tail-cups*. The comparison of subgroup *a* (always access to faeces) with subgroup *c* (permanent tail-cups) in Expt 1 gave a small but highly variable amount of coprophagy. The high percentage in the seventh week was due to an unexplained low food consumption in subgroup *c*. If this value is omitted, the rats ate 6 (range 1–11)% of their faeces. In Expt 2 subgroup *a* can only be compared with the periodically prevented rats of subgroups *b* and *c* (Table 4). This gives consistently negative values for faeces consumption up to −25%. The periodically prevented rats are, therefore, not suitable as reference animals for unrestricted rats.

(b) *Rats with tail-cups every second week*. When the values for these rats during the weeks without tail-cups were compared with those from rats wearing tail-cups permanently (Expt 1, subgroup *c*) or with their prevented group-mates, they showed consistent coprophagy. The amounts were 19 (range 16–22)% in Expt 1 and 15 (range 7–18)% in Expt 2. Intermittent prevention of coprophagy thus increased the amount of faeces eaten during the weeks without tail-cups.

When using model 2A, the comparison with the previous week gave almost the same results as comparison with the subsequent week. In the majority of weeks of the study the rats ate 12–28% of their faeces; the average was 18% (Table 4).

Effects and after-effects of the prevention of coprophagy

In rats permanently without or with tail-cups the daily food consumption and faeces excretion varied at random. In several of the periodically prevented rats, however, there were distinct trends in food intake and faeces excretion within the 7 d periods with, and within periods without, tail-cups (subgroup *b* in group C, subgroups *b* and *c* in group F). The animals ate either more or less during the first 2 d after the tail-cups were fixed. Faecal excretion was higher during the first 2 d with tail-cups than during the subsequent 5 d. Less faeces could be collected during days 1 and 2 after removal of the tail-cups. This reduction in the amount of faeces (by 27–39%) occurred in spite of normal food intake and indicated increased coprophagy on these 2 d. Similarly, the daily rates of coprophagy calculated for

Table 3. *Mean values and coefficients of variation (CV, %) of daily food intake and faeces production from rats fed on the control diet and kept alternately with and without tail-cups*‡

(Mean values from 21 to 28 d. Weights expressed on a dry matter basis)

Expt no.	Sub-group	Rat no.	Food intake (g)				Faeces collected (g)				Coprophagy§ (g)	
			Without tail-cup		With tail-cup		Without tail-cup		With tail-cup			
			Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	%
1	*b*	13	17·5	16	16·0*	15	1·64	41††	1·88	23	0·42	20
		14	17·8	14	16·3*	14	1·76	36†††	1·95	17	0·37	17
2	*b*+*c*	13	16·4	12	16·1	8	1·51	33††	1·78*	18	0·30	17
		14	16·6	11	16·5	9	1·48	26	1·82**	26	0·35	19
		15	16·9	12	16·2	11	1·69	28	1·74	25	0·13	7
		16	17·5	9	16·5*	10	1·51	28†	1·83**	20	0·43	22
	Mean	*n* 140 (six animals, 140 d)	17·1	—	16·3*** (−5%)	—	1·60	—	1·83*** (+14%)	—	0·33	17

Differences between animals with and without tail-cups were significant: * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$.
CV was significantly greater for animals without tail-cups than those with tail-cups: † $P < 0{\cdot}05$, †† $P < 0{\cdot}01$, ††† $P < 0{\cdot}001$.
‡ For details of diet and procedures, see pp. 552–554 and Table 1.
§ Calculated according to model 2A and expressed as percentage of all faeces produced.

Table 4. *Coprophagy of rats on the control diet (Expt 1, group C; Expt 2, group F), calculated in different ways* as illustrated in Fig. 1*

(Values are expressed as percentage of all faeces produced)

	Model*	Reference subgroup*	Dietary group	Rat no.	Week no. 1	2	3	4	5	6	7
(1)	Rats continuously without tail-cups (subgroup *a*)										
	2B	*c*	C	17+18	10·8	2·1	10·3	8·0	2·8	1·1	(27·7)
	2B	*b*+*c*	F	17+18†	−8·3	−3·5	−4·7	−12·6	−23·0	0·0	−24·6
(2)	Rats with tail-cups every second week										
	2B	*c*	C	13+14	—	16·1	—	22·1	—	18·5	—
	2B	*b*+*c*	F	‡	17·3	13·1	15·7	17·8	6·9	15·9	18·4
	2A	‹	C	13	—	14·4	—	21·0	—	22·9	—
	2A	‹	C	14	—	3·9	—	27·7	—	14·5	—
	2A	›	C	13	—	26·8	—	21·6	—	17·2	—
	2A	›	C	14	—	19·6	—	22·0	—	27·3	—
	2A	‹	F	13	—	28·9	—	14·8	—	14·2	—
	2A	‹	F	14	—	22·3	—	24·5	—	10·1	—
	2A	‹	F	15	—	−11·3	—	20·9	—	11·7	—
	2A	‹	F	16	—	17·3	—	25·2	—	27·8	—
	2A	›	F	13	—	12·4	—	1·3	—	16·1	—
	2A	›	F	14	—	25·3	—	16·9	—	16·1	—
	2A	›	F	15	—	27·0	—	16·5	—	−5·8	—
	2A	›	F	16	—	21·1	—	12·4	—	33·1	—

‹, Comparison with previous week; ›, comparison with following week.

* For details of groups, models and calculations, see pp. 552–553.

† Rats with the same numbers in groups C and F were not identical.

‡ 13+14 (weeks 1, 3, 5, 7) and 15+16 (weeks 2, 4, 6).

Table 5. *Coprophagy of rats on the experimental diets*†

(Each value is calculated according to model 2B (for details, see p. 553) from the weekly pooled values for food intake and faeces excretion of two rats. Mean values and standard deviations)

	Rats without tail-cups			Rats with tail-cups every second week		
	Amount (g/d)			Amount (g/d)		
Diet	Mean	SD	%	Mean	SD	%
Control	0·25	0·32	10·0	0·40	0·10	19·0
Low-protein (62·5 g/kg)	0·06	0·13	3·2	0·44**	0·11	18·5
High-cellulose (200 g/kg)	0·32	0·18	7·9	0·59	0·28	12·2
Thiamin-deficient	0·55	0·55	29·1	1·21	0·75	52·7
Pantothenate-deficient	0·55	0·16	24·3	0·62	0·28	29·7

Significantly different from animals without tail-cups: ** $P < 0·01$.

† For details, see pp. 552–554 and Table 1.

subgroup *b* for the 3 weeks without tail-cups by using the permanently prevented rats as a reference indicated augmented re-ingestion during the first 2 d.

Coprophagy of rats with the experimental diets (*Table 5*)

In protein deficiency the amount of faeces eaten was small and variable. It did not differ significantly from that in the rats on the control diet. The rats with tail-cups every second week consumed seven times as much faeces as the rats with free access to their excreta. When the cellulose content in the diet was raised to 200 g/kg the rats ate consistently small amounts of their faeces: 8% in the rats without tail-cups and 12% in rats with tail-cups every second week. These values were not significantly different from those for the control diet group. In thiamin deficiency faeces consumption was variable but generally large; the averages were 29% for the unprevented subgroup *a* and 53% for the intermittently prevented subgroups *b* and *c*. The latter groups consumed up to 85% of their faeces; this was the highest percentage found with any diet. The diet deficient in pantothenate induced large and very consistent rates of coprophagy. They were, however, not significantly higher in the intermittently prevented group (29%) than in the group with continuous access to its faeces (25%). In spite of the fact that the state of health of the vitamin-deficient animals deteriorated during the 7 weeks as seen from the reduced growth rates, no trend was seen towards progressively higher re-ingestion. Such a trend was also absent in the other diet groups.

DISCUSSION

The application of a tail-cup reduced food intake and weight gain in most of the rats. The amount of faeces produced by these rats is, therefore, only comparable when corrected for differences in food consumption (model 2). Model 1 was not applicable. Although a reduced food consumption of rats in which coprophagy was prevented was also found in most previous studies, no such correction was applied when calculating the extent of coprophagy, with the exception of Araja *et al.* (1973), who corrected faecal output according to food consumption. With such a correction, the relatively high re-ingestion found by Barnes (1962) in several of his studies would become even higher.

In experiments of the type reported here, attempts are made to estimate the quantity of re-ingested faeces by subtracting the amount of faeces collected in control rats from the amount obtained from the same or other rats fitted with tail-cups, but kept under otherwise

comparable conditions. This difference is inevitably subject to random error due to biological and methodological variations. Biological variability results from day-to-day differences in food intake and gastrointestinal passage time. Excretion of faeces is therefore more variable than food intake. The gain in accuracy by correcting faecal output for variations in food intake, as used in model 2, is therefore limited.

The quantity of faeces re-ingested varies from day to day. This is indicated by the fact that the variability of faecal dry-matter output in rats without tail-cups is much higher than in rats with tail-cups, in spite of comparable variability in food intake of both groups. Because of the previously mentioned variability it is not possible to obtain an accurate value for the amount of faeces eaten by an individual rat on a particular day. Pooling of the values for at least two rats and for at least 7 d is desirable before model 2B is applied. Comparison of different rats kept under comparable conditions (model 2B) reduces systematic errors caused by changes of the physiological state of the animals over the experimental period, but retains individual differences. Comparison of an animal with itself (model 2A) can be made with 7 d averages. This approach avoids between individual effects, but the results may be affected by systematic trends in the physiological state.

Systematic errors in the calculated difference due to shifts in the level of food intake and changes in digestibility are of minor importance. Dry-matter digestibility of the control diet was 88·8 % without and 87·7 % with tail-cups (difference not significant) and did not change during the 7 weeks.

The percentage coprophagy found in the present study was generally lower than the values obtained in experiments carried out several decades ago (Roscoe, 1931; Mameesh & Johnson, 1959; Mameesh *et al.* 1959; Barnes, 1962). This may reflect differences in the type of animal and in the quality of the diet as well as differences in methodology. Takahashi *et al.* (1985) reported strain differences in percentage coprophagy for mice. The higher growth rates in our animals suggest our control diet to be more complete and better balanced than the diets used in previous studies.

The consumption of faeces is normal physiological behaviour in rats. It does not disappear on a nutritionally complete and balanced diet. Preventing rats from eating faeces induces a deficiency state which is compensated as soon as the animals gain access to faeces. Most of the deficit is made up during the first 2–3 d after removal of the tail-cup. During this time 20–30 % of all faeces may be consumed. However, individual rats react in unpredictable ways with respect to their food consumption. Thus comparing the amount of faeces from 1–2 d with and the subsequent 1–2 d without tail-cups, or in the reverse sequence, is no reliable basis for calculating rates of coprophagy. Long-term prevention of coprophagy gives more stable conditions suitable as a reference for calculating re-ingestion. However, on diets deficient in essential nutrients prevention of coprophagy can lead to rapid deterioration in the condition of the animals, with loss of appetite, reduced growth or even weight loss. This renders the reference group less and less suitable for comparison with the control group. Under such conditions the divergence of the two groups can be slowed by preventing coprophagy every second week or by giving access to faeces from the control group.

Using rats with tail-cups every second week as control animals leads always to high re-ingestion rates, when only the weeks without tail-cups are considered. But over the total experimental period (weeks with and without tail-cups) the rats ate about the same amount of faeces as rats with continuous access to their excreta. This holds, with some variations, also in the experimental diet groups. It can be concluded that rats require a certain amount of faeces which depends on the nutritional quality of their diet. The ingestion of this amount is guaranteed by unknown regulatory mechanisms in spite of day-to-day variations and even under conditions of temporary prevention.

The increased consumption of faeces during thiamin and pantothenate deficiency

indicates that coprophagy is a regulated phenomenon. It was unexpected to find no increased re-ingestion in the low-protein group. This may be because the protein deficiency was not severe and still permitted continuous growth. In a separate experiment not reported here coprophagy was measured in rats on a protein-free diet and found to be important (28%) (Fajardo, 1987). The same trend was observed by Araja *et al.* (1973): 12% coprophagy with 100 g protein/kg diet, 0% with 40 g protein/kg, 36% with protein-free diet. The findings indicate that, except for extreme conditions, rats regulate their re-ingestion rate primarily to meet their vitamin requirements. The bacterial protein synthesized in the hind gut seems of minor nutritional importance.

Dilution of the diet with cellulose is compensated by a higher food consumption. The bulk of the faeces was increased. The percentage coprophagy remained in the range of the control animals but, due to the larger mass of faeces produced, the absolute amount of faeces eaten was higher than in the controls.

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