STUDIES ON MARSUPIAL NUTRITION

II. THE RATE OF PASSAGE OF FOOD RESIDUES AND DIGESTIBILITY OF CRUDE FIBRE AND PROTEIN BY THE QUOKKA, SETONIX BRACHYURUS (QUOY & GAIMARD)

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Summary

The rate of passage of food residues through the digestive tract of a small grazing marsupial, *Setonix brachyurus* (Quoy & Gaimard) was determined. The animals were fed various mixtures of lucerne chaff, concentrates, and oaten chaff. The marked meal generally first appeared in the faeces 8–12 hr after feeding; 90 per cent. was excreted in about $1\frac{1}{2}$–$2\frac{1}{2}$ days and the meal was usually totally eliminated in 3–6 days. The rate of passage was slower with low food intake than with high food intake, and also with relatively coarser food. *S. brachyurus* excretes food residues in a pattern similar to that of domestic ruminants but at a faster rate, particularly in the terminal stages.

Digestibility of dry matter was 51–68 per cent., of crude fibre 25–48 per cent., and of crude protein 64–79 per cent. of the intake of the particular rations fed. When compared with domestic herbivores, fibre was digested considerably less efficiently by *S. brachyurus* than by ruminants but more efficiently than by the rabbit. The ability to digest crude protein was within the same range as for other herbivores for which figures are available. It is concluded from this work that *S. brachyurus* is intermediate in its digestive efficiency between the ruminants and non-ruminant herbivores.

I. INTRODUCTION

Moir, Somers, and Waring (1956) have reported on the digestive physiology of the quokka, *Setonix brachyurus* (Quoy & Gaimard), a small grazing macropodid. The various features described—large sacculated stomach with an oesophageal groove, fermentation of food by bacteria with the production of organic acids, absorption of these acids, and low blood sugar levels—led these authors to conclude that the digestion pattern was ruminant-like.

Two associated characteristics of ruminant digestion are the long time food is retained in the tract and the efficient digestion of fibre. In the cow, sheep, and goat, for example, food residues are held in the rumen for several days, and it takes 2–4 days or more for 80 per cent. of the material to be excreted (Balch 1950; Blaxter, Graham, and Wainman 1956; Castle 1956*a*). In non-ruminant herbivores such as the horse, on the other hand, most if not all of the food residue is excreted in 24–48 hr (Alexander 1946). The digestibility of fibre is related to the time it spends in the digestive tract. Watson and Godden (1935) showed, for example, that the digestibility of crude fibre of artificially dried pasture was only 26·0 per cent. in the rabbit compared with 74·5 per cent. for the sheep.

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It was therefore of interest to investigate these related features of herbivore digestion in the quokka. A series of fibre-digestibility and rate-of-passage experiments using various diets is described in this paper. Crude protein digestibility and the nitrogen balance were also determined at the same time as fibre digestibility.

II. Experimental

(a) *Animals*

All experiments were done with wild male quokkas from Rottnest I. The animals were kept separately or in pairs, in yards equipped with small shelters, for a few weeks after capture to accustom them to humans and handling. The age was unknown but dental examination showed they were prime adults. It was presumed that all had a "normal" small infestation of the nematode *Austrostrongylus thylogale* Johnston & Mawson, which is found in quokkas taken on the island.

(b) *Cages and Collection of Excretion Products*

The animals were kept individually in $1\frac{1}{4}$-in. mesh cages, 2 ft 6 in. long and 1 ft 3 in. square in cross section, placed on a rack about 3 ft above the floor. The quokka presented some difficulties for this type of investigation because of its habits of raking through the food and of carrying the food about in its fore paws. A special food container was devised to overcome this as much as possible. This consisted essentially of a small tin inside a large one with high sides and back, and with the front edges of both tins turned inwards. This arrangement prevented food spillage but there seemed no way of preventing food being carried away. This behaviour was subject to great individual variation and unsatisfactory animals were not used. A small piece of board on which the animals liked to rest was placed in each cage.

For the collection of faeces and urine, a long tray which sloped steeply from back to front was placed under each cage. The tray had a spout at the lower end and a piece of plastic tubing connected to it ran into a bottle. Covering the tray was a screen of fly-wire mounted on a wooden frame. The urine passed through the wire and the faecal pellets rolled down to the bottom end of the screen and were caught against a baffle board. The small amount of food dropped on to the screens was dried and weighed for computing food intake but was not used in samples for analysis.

Throughout the experiment the animals were weighed every two or three days, at the same time each day.

(c) *Diets*

In the holding yards the animals were provided with sheep nuts* (a proprietary pelleted concentrate containing about 20 per cent. crude protein and $7\frac{1}{2}$ per cent. crude fibre) and water *ad lib*. From casual observations on caged animals it seems that a diet of sheep nuts alone may be detrimental to quokkas and some showed symptoms suggestive of ammonia poisoning. However, sufficient fibre was obtained from dried leaves, twigs, and bark of *Eucalyptus*, *Banksia*, etc. which littered the yards. On this abundant high protein diet the animals became very fat.

*"Ewe and Lamb Sheep Nuts", manufactured by Hemphill Gray Oil Mills, Perth.

The quokkas could not be induced to eat any of the usual dried foodstuffs, such as grass or hay. In preliminary trials in cages, several samples of long or chaffed grass hay and oaten hay were offered but the animals ate very little and in fact would starve to death rather than eat the material. In one rate-of-passage experiment (RP1), a sample of oaten chaff in conjunction with sheep nuts and a small proportion of lucerne chaff, was eaten in sufficient amounts to maintain the weights of five out of six animals. Unfortunately no more of this material could be obtained for a digestibility trial. This particular sample was singularly free from insect and mould attack; all other samples of oaten chaff were slightly contaminated with one or the other.

Because of these difficulties the diets used were based on lucerne chaff which was readily accepted. The lucerne chaff was of good quality and contained 3·16 per cent. nitrogen and 27·6 per cent. crude fibre, determined on a dry weight basis. In experiment RP1 the animals were given 39 g of sheep nuts daily, all of which were eaten, and a mixture of seven parts of oaten chaff to one part of lucerne chaff *ad lib.* The food offered in experiments RP2 and D2 (D = digestion) was lucerne chaff alone. In experiments RP3 and D3 the food given was lucerne chaff intimately mixed with ground sheep nuts in the proportion of 3 : 1. The mixture contained 3·21 per cent. nitrogen and 25·1 per cent. crude fibre. The offering in experiments RP4 and D4 was equal parts of oaten chaff, lucerne chaff, and ground sheep nuts intimately mixed. Assay of the mixture gave 2·51 per cent. nitrogen and 20·8 per cent. crude fibre. These mixtures were chosen to vary the proportions of crude fibre and protein in the diet.

It was observed that quokkas often ejected a bolus of partly digested food which was re-eaten immediately. In the cages this fell through the wire and could not be recovered by the animal. There are no unequivocal observations of rumination by macropodids, but it is possible that the bolus is digesta which has been regurgitated in a manner analogous to the process in rumination. Quokkas were very variable in this behaviour. One individual produced a bolus every other day while others produced a bolus once in 10 days. It is possible that the regurgitation takes place more frequently than observed and that usually the bolus is not dropped from the mouth. During rate-of-passage experiments the bolus was discarded; however, it was fed back during digestibility trials and was almost always eaten immediately, even though the animal was not feeding at the time.

(*d*) *Rate-of-passage Experiments*

For 3 weeks prior to the commencement of an experiment the animals were fed on the diet to be tested.

The method employed for measuring the rate of passage was an adaptation of that of Balch (1950) in which a small single meal stained with a dye is given to the animal and undigested dyed particles are identified visually in the faeces and counted. In all experiments quokkas were given 3–4 g of a moistened mixture of dyed chaff and a small amount of ground sheep nut. This was eaten in 10–20 min, the mid-point being taken as the starting time of the experiment. Brilliant green was the most satisfactory of a number of dyes tested.

Faeces were collected 8 hr later, every 4 hr for the next 2 days, and then at progressively longer intervals until no further coloured particles were being excreted. The total faeces for any collecting period were weighed, broken up and well mixed, and four 2·5-g samples were weighed out for counting. The preparation of the samples and counting technique were according to Balch. The total number of coloured particles excreted in each collection period was calculated and each period total was expressed as a percentage of the grand total. The cumulative percentages were plotted against time to give excretion curves.

TABLE 1

RATES OF EXCRETION OF FOOD RESIDUES BY QUOKKAS FED DIFFERENT DIETS

Expt. No. and Diet	Animal No.	Body Weight (g)	Dry Matter Intake (g/day)	Time of:			
				First Appearance (hr)	5% Excretion (hr)	90% Excretion (hr)	Last Appearance (hr)
RP1—39 g sheep nuts and 7 : 1 mixture of oaten and lucerne chaff *ad lib*	1	3170	93	12	13	47	112
	2	2650	62	16	18	66	140
	3	3560	120	16	16	46	120
	4	3810	107	12	12	47	104
	5	3380	98	20	20	57	120
	6	3120	113	12	14	48	104
RP2—lucerne chaff	1	3460	116	8	12	34	104
	3	3480	138	12	12	36	68
	4	3900	112	8	14	38	88
	6	3340	119	12	17	42	96
RP3—3 : 1 mixture of lucerne chaff and sheep nuts	7	3740	120	8	9	41	88
	8	3230	112	12	<12	43	88
	9	3850	124	8	<8	39	88
	10	3780	108	12	13	43	72
RP4—equal parts of oaten and lucerne chaff and sheep nuts	1	3330	60	8	13	58	216*
	4	3790	74	8	13	62	144
	8	3670	44	8	11	53	136
	10	3720	46	16	19	67	144

*In this animal the last appearance of coloured particles appeared to be 144 hr. However, a single coarse coloured particle which had apparently become caught in the tract was observed at 216 hr.

(*e*) *Digestibility Trials*

At the end of the rate-of-passage experiment, a digestibility trial was started immediately, using the same animals and diet. The trial lasted 10 days. The excretion products were collected daily at feeding time (4 p.m.). The faeces were dried in an oven at 105°C and weighed when oven dry. The whole output for 10 days was broken up and mixed thoroughly and a sample taken for analysis. The 24-hr urine sample was made up to 200 ml or 1 l. with water and sulphuric acid so that the final solution was 1N with respect to acid. 20-ml aliquots were taken daily, bulked, and stored at 0°C under toluene for analysis.

The unconsumed food was also collected daily and bulked, and at the conclusion of the experiment the total unconsumed food for each animal was weighed and a sample taken for analysis. This was necessary because some at least of the quokkas were able to effect a partial separation of the high protein components such as lucerne leaves and ground sheep nuts from the rest of the food.

The samples of food, unconsumed food, and faeces for analysis were ground in a Wiley mill and stored in air-tight jars.

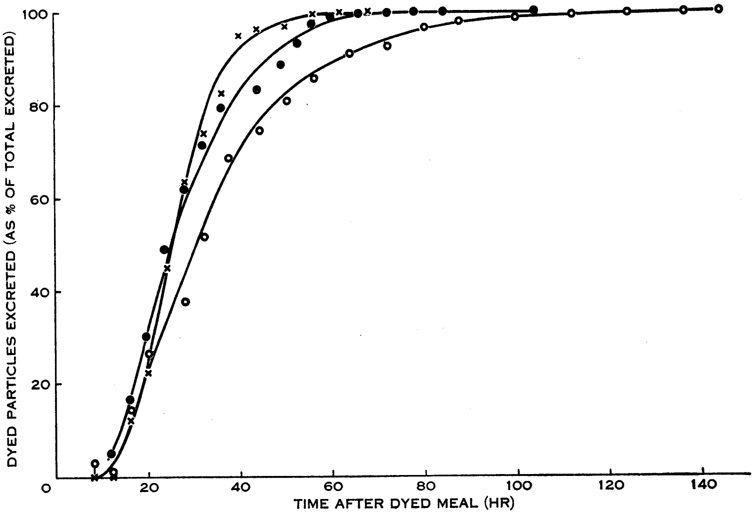

Fig. 1.—Rate-of-passage curves for one quokka (No. 4) fed different diets. ● Experiment RP1: daily intake of 39 g sheep nuts, plus 68 g of 7 : 1 oaten and lucerne chaff mixture. × Experiment RP2: daily intake of 112 g of lucerne chaff. ○ Experiment RP4: daily intake of 74 g of mixture of equal parts of oaten and lucerne chaff and sheep nuts.

(*f*) *Chemical Analyses*

Nitrogen, crude fibre, and moisture analyses were done by standard methods recommended by the Association of Official Agricultural Chemists (1950). Nitrogen was determined in 1-g samples of food, unconsumed food, and faeces. 2-g samples were used for crude fibre and moisture analyses. For urinary nitrogen, 2-ml aliquots were taken when the daily sample had been made up to 200 ml and 10-ml aliquots when the daily sample had been made up to 1 l.

III. Results

(*a*) *Rate-of-passage Experiments*

Relevant data on the rate of passage of food residues are given in Table 1. The body weights recorded are the average weights of the animals during the course of the rate-of-passage experiment.

TABLE 2

DIGESTIBILITY COEFFICIENTS AND ASSOCIATED DATA FOR QUOKKAS FED DIFFERENT DIETS

	Experiment D2—Lucerne Chaff				Experiment D3—3 :1 Mixture of Lucerne Chaff and Sheep Nuts				Experiment D4—Equal Parts of Oaten and Lucerne Chaff and Sheep Nuts			
	Animal No.				Animal No.				Animal No.			
	1	3	4	6	7	8	9	10	1	4	8	10
Dry matter intake (g/day)	116·3	138·4	112·3	119·3	119·8	111·6	123·7	107·6	59·6	74·4	44·2	45·6
Dry faeces (g/day)	46·8	57·1	46·7	48·2	40·5	39·6	45·6	34·1	25·7	31·2	21·6	17·4
Nitrogen intake (g/day)	3·90	4·56	3·73	3·93	4·14	3·84	4·05	3·65	1·69	2·09	1·29	1·58
Nitrogen in faeces (g/day)	0·93	1·13	0·81	0·98	0·98	0·90	1·03	0·78	0·57	0·66	0·47	0·45
Nitrogen in urine (g/day)	2·17	2·50	2·25	1·97	2·39	2·25	2·25	2·63	1·33	1·36	1·42	1·34
Nitrogen balance (g/day)	+0·80	+0·94	+0·67	+0·98	+0·78	+0·70	+0·77	+0·24	−0·21	+0·07	−0·60	−0·21
Crude fibre intake (g/day)	29·7	35·6	28·6	29·8	23·4	25·0	29·9	24·1	11·9	11·3	8·9	8·7
Dry matter digestibility (%)	59·8	58·7	58·3	59·6	66·2	64·5	63·1	68·2	56·9	58·0	51·1	61·8
Crude fibre digestibility (%)	32·3	29·9	25·1	31·8	39·2	40·6	41·0	46·6	46·5	30·6	33·0	48·1
Crude protein digestibility)%)	76·2	75·2	78·3	75·1	76·3	76·6	74·6	78·6	66·3	68·4	63·6	67·3
Weights of animals (g)	3490^{+30}_{-0}	3510^{+0}_{-30}	3830^{+90}_{-90}	3320^{+90}_{-0}	3680^{+90}_{-0}	3230^{+90}_{-0}	3850^{+0}_{-110}	3740^{+60}_{-0}	3280^{+30}_{-20}	3740^{+90}_{-0}	3660^{+0}_{-430}	3640^{+0}_{-60}

All curves of the excretion of marked meals by quokkas are similar in form, and are of the same general shape as those of domestic ruminants (Balch 1950; Blaxter, Graham, and Wainman 1956; Castle 1956*a*).

The rate-of-passage curves obtained for one animal (No. 4) used in three experiments, are shown in Figure 1. The shape of each of these curves is typical for all of the animals in the corresponding experiments in which this animal was used. The rate of passage of this animal was one of the fastest in experiment RP1 but was intermediate in experiments RP2 and RP4.

(*b*) *Digestibility*

Table 2 gives digestibility coefficients (i.e. the amount of nutrient digested, found by subtracting the content in the faeces from the amount in the intake, expressed as a percentage of the intake of the particular nutrient) and associated information on digestibilities and nitrogen balance. The weights of the animals at the start of the experiment are given, together with maximum departure from this weight during the 10 days of the experiment.

Within each experiment the dry matter and crude protein digestibilities of the animals are very similar. However, there is considerable variability between animals in their ability to digest crude fibre.

The crude protein digestibilities are lower in experiment D4 than in the two earlier experiments. The nitrogen content of this diet was much lower than in any of the previous diets.

IV. Discussion

It is of interest to compare the rate of passage through the digestive tract and digestibility coefficients in the quokka with published values on domestic ruminants and non-ruminant herbivores. The results are not strictly comparable as the nature and composition of the foods given are not the same. Nevertheless, some interesting comparisons may be made.

From an examination of results published by Balch (1950) who determined the rate of passage through dairy cows fed grass hay with or without various additions, it is seen that cows excrete food residues at a much slower rate than quokkas. Blaxter, Graham, and Wainman (1956) performed a series of tests with sheep fed different amounts of long, medium, or ground grass hay. All sheep on medium length grass, irrespective of the amount fed, have a slower rate of passage than the quokkas in experiment RP4; sheep fed long grass have an even slower rate.

The rates of passage for the well-fed quokkas in the first three experiments are fairly close to, or slightly slower than, the sheep having the fastest passage (those fed finely ground food in greatest amount) up to about 24–30 hr. After this time the passage through the sheep becomes considerably slower. The quokkas in experiment RP4 have a slower passage rate than these sheep up to about 36 hr. After this the sheep are close to the quokkas although the time before the marked meal is completely excreted is greater in the sheep.

Two of the factors influencing the rate of passage of food residues in the sheep, namely the degree of fineness and degree of fill, appeared to operate in the quokka.

TABLE 3

DIGESTIBILITY COEFFICIENTS FROM THE LITERATURE

Species	Authority	Food	Dry Weight Analysis (%)		Digestibility Coefficients (%)		
			Crude Protein	Crude Fibre	Dry Matter	Crude Protein	Crude Fibre
Quokka	This paper	Lucerne chaff	20·6–20·9	25·0–25·7	58·3–59·8	75·1–78·3	25·1–32·3
		Lucerne chaff and sheep nuts; lucerne and oaten chaff and sheep nuts	17·6–21·6	15·2–24·2	51·1–68·2	63·6–78·6	30·6–48·3
Sheep	Watson and Godden (1935)	Artificially dried pasture herbage	20·8–20·9	21·3–21·6	74·3	76·4–76·9	73·5–74·5
Sheep	Watson and Horton (1936)	Grass (several samples)		22	72·2–77·7	75·8–81·0	78·3–84·0
Sheep	Louw (1944)	Lucerne hay	14·9–18·4		57·3–67·8	75·8–81·7	
Sheep	Swift *et al.* (1950)	Lucerne	23·9	25·1	61·9	74·5	48·9
Cattle (dairy shorthorn cows)	Balch (1950)	Grass hay, variously ground, with or without concentrates			58·2–70·8	47·8–67·3	36·3–74·8
Cattle (dairy shorthorn cows)	Balch *et al.* (1953)	Lucerne hay	13·8	38·2	56·7–63·5	68·1–73·4	53·5–62·8
Cattle (Holstein heifers)	Swanson and Herman (1952)	Lucerne, variously ground	14·8	35·8	54·1–60·0	67·6–73·2	37·9–48·8
Cattle (steers)	Crampton *et al.* (1940)	Chaffed pasture herbage	27·1–29·5	15·0–17·6	62–70	72–77	65–77
Cattle (Afrikaner steers)	Groenewald *et al.* (1950, 1952)	Lucerne hay	17·1–18·3	29·2–30·7	54·8–63·9	71·3–77·3	32·0–49·3
Deer (*Odocoileus hemionus* (Rafinesque))	Bissell *et al.* (1955)	Lucerne hay	14·3–15·9			67·9–75·1	
Rabbit	Voris *et al.* (1940)	Lucerne chaff	20·1–30·3	21·8–34·9	48·1–67·5	72·3–83·6	18·2–29·8
Rabbit	Watson and Godden (1935)	Artificially dried pasture herbage	20·8–20·9	21·3–21·6	45·6–50·9	60·8–64·3	21·3–28·7
Rabbit	Watson and Horton (1936)	Grass (several samples)		22	62·8–63·4	76·2–79·0	46·9–51·0
Rabbit	Crampton *et al.* (1940)	Chaffed pasture herbage	27·1–29·5	15·0–17·6	45–53	65–70	24–31

The 90 per cent. elimination times were longer in experiment RP1 where the material fed was relatively coarser, and also in experiment RP4 where the intakes were considerably reduced below those in experiments RP2 and RP3.

Castle (1956*a*) has worked with goats using meadow hay and concentrates as food. Generally the rate of passage in goats was slower than in quokkas. Castle quotes earlier workers who obtained much slower rates of passage in goats and in later papers (1956*b*, 1956*c*) obtained somewhat slower rates herself with a few animals.

Little information is available on the rate of passage of food residues in non-ruminant herbivores. Alexander (1946) experimented with horses fed oats and bran using carbon granules as a marker. He found that the marker appeared in the faeces 22 hr after feeding and was completely eliminated by 48 hr (means of 17 separate observations on five different animals). The only experiment on the rabbit known to the author (cf. Elliott and Barclay-Smith 1904) is not comparable since the glass beads used do not fulfil the requirements of a satisfactory marker (Alexander 1946).

It is evident that undigested food residues are excreted by the quokka in a manner similar to that of ruminants but at a faster rate particularly in the later stages. The slow elimination in the later stages is a characteristic of ruminants.

In Table 3, digestibility coefficients of standard feeding stuffs, particularly lucerne, from experiments on the quokka, ruminants, and the rabbit, are listed from the literature. The relative digestion efficiency of the rabbit and ruminants is best illustrated by the work of C. J. Watson and Godden (1935), S. J. Watson and Horton (1936), and Crampton, Campbell, and Lange (1940) who compared sheep or cattle with rabbits fed identical diets. In these comparative studies the protein digestion coefficients for the ruminants are consistently higher than those for the rabbits. From the values in Table 3 it may be seen that all species (including the quokka) digest the crude protein of good quality diets efficiently.

The relative ability of ruminant and non-ruminant herbivores to digest crude fibre is reasonably clear-cut, and in this regard the quokka is considerably less efficient than ruminants, but more efficient than the rabbit. Morrison (1938) states that the horse is somewhat less efficient than ruminants at digesting feed, particularly fibre. Alexander (1952) using the *in vivo* cotton-thread technique of Balch and Johnson (1950) showed that the capacity of the organisms in the large intestine of the horse to ferment cellulose is not inferior to those of the rumen of the cow. The degree of digestion therefore depends upon the time for which the cellulosic material is exposed to the fermentation.

In ruminants, the time taken by the food to pass through the tract is largely spent in the rumen where the food undergoes active digestion. Because of differences in stomach anatomy and presumably movements, the pathway of food in the rumen is more complex than in the simpler stomach of the quokka. No determination was made of the time the food was in the quokka stomach but it is probably appreciable in terms of the total length of the alimentary tract, assuming that the digestive efficiency of the ruminant rumen is similar to that of the quokka stomach plus caecum. The fact that digestion of fibre by the quokka is intermediate between the two herbivore types suggests, too, that the length of stay of food in the quokka stomach is longer than in the caecum, assuming that the rate of movement through the rest of the gut is of the same order in the two types.

In the quokka, not only is the rate of passage faster than in ruminants, but the digestibility of fibre is considerably lower. The quokka therefore occupies an intermediate position between the ruminants and non-ruminant herbivores with regard to the related characteristics—rate of passage and efficient digestion of fibre.

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