Fermentation in the Hindgut of the Greater Glider (*Petauroides volans*) and the Brushtail Possum (*Trichosurus vulpecula*)—Two Arboreal Folivores

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Abstract

*The pattern and rate of microbial fermentation were studied in captive and wild-shot greater gliders (*Petauroides volans*) and captive brushtail possums (*Trichosurus vulpecula*) fed* Eucalyptus *foliage. The cecum and the cecum/proximal colon were the principal sites of microbial activity in the greater glider and brushtail possum, respectively. Total short-chain fatty acid (SCFA) concentrations were 36 mM and 70 mM in captive and wild-shot greater gliders, respectively, and 75 mM in the brushtail possums. SCFA production rates in the hindgut were similar in vitro in the two species (19–20 mmol/L/h) but slower than in the hindgut of most herbivores, although this was offset by the large volume of digesta contained in the hindgut. The pattern and rate of fermentation were similar in captive and wild-shot greater gliders. The difference between the initial molar proportions of acetate, propionate, and butyrate and their proportional contributions to total SCFA production in both species suggested that SCFAs were absorbed in proportion to their chain length. SCFA production contributed similar amounts of energy to both species, but as a proportion of digestible energy (DE) intake, SCFA was 15% of the DE intake of the brushtail possum and 7% of the DE intake of greater gliders. The relatively low level of SCFA production in both greater gliders and brushtail possums is largely due to the lignified nature of the fiber of* Eucalyptus *leaves and, in the brushtail possum at least, the inhibitory effects of leaf phenolics.*

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Introduction

The greater glider (1–1.5 kg) and the brushtail possum (2–4 kg) are small nocturnal arboreal marsupials. Whereas the greater glider feeds almost exclusively on *Eucalyptus* leaves (Marples 1973; Kehl and Borsboom 1984; Henry 1985), the brushtail possum consumes a more varied diet, with fruit, flowers, and herbage supplementing *Eucalyptus* leaves in most parts of its range (Kerle 1984). Anatomical and microscopic observations (Foley 1987; Foley and Hume 1987*a*) suggest that fermentation of plant structural carbohydrates occurs in the hindgut of both species. The stomach is relatively small and simple in both species, but the cecum of the greater glider is large and extensively haustrated. In the brushtail possum, both the cecum and the proximal colon are enlarged but, in contrast to those of the greater glider, are not notably haustrated.

Previous studies of the digestion of *Eucalyptus* leaves in these and other species of arboreal marsupials have shown that 25%–43% of the cell walls of the diet are digested (Cork, Hume, and Dawson 1983; Chilcott and Hume 1984; Foley 1987; Foley and Hume 1987*a*). Several factors, including the high lignin content of *Eucalyptus* leaves, the pattern of mastication, and the practice of cecotrophy by one species, the ringtail possum (Chilcott and Hume 1985), have been suggested as contributing to this low and variable digestion (Foley 1987). To date, differences between species in the nature of the fermentative processes have not been considered.

As well as a high fiber content, *Eucalyptus* foliage has significant quantities of essential oils and polyphenols (Fox and MacCauley 1977; Morrow and Fox 1980). Both these groups of allelochemicals have the potential to affect fiber digestibility through their impact on microbial activity (Nagy and Tengerdy 1968; Palo 1985). However, in both greater gliders and brushtail possums, essential oil-microbe interactions are largely avoided because little ingested oil reaches the hindgut (Foley, Lassak, and Brophy 1987). On the other hand, tannins have been shown to have significant inhibitory effects on the intake and digestibility of cell walls in the brushtail possum (Foley and Hume 1987*a*).

This study was undertaken to examine the nature and importance of fermentative digestion in the greater glider and brushtail possum. Initially, we made measurements of the concentration and production rates of short-chain fatty acids (SCFAs) in the hindgut of captive animals fed natural foliage diets. Because we were surprised at the low concentrations and the low production rate of SCFA in the cecum of the greater gliders, we followed

this laboratory study by measuring cecal SCFA concentrations and production rates in greater gliders feeding actively in the field.

Material and Methods

Laboratory Study

Six greater gliders were caught during logging operations in the Nundle State Forest, 100 km southeast of Armidale. Four male brushtail possums were caught in cage traps in *Eucalyptus* woodland near Armidale. All animals were maintained in large outdoor enclosures, on a diet of *E. radiata* foliage in the case of the greater gliders and *E. melliodora* foliage for the brushtail possums. Different foliages were necessary, since the animals would eat no diet in common (Foley and Hume 1987*b*). Nonetheless, we do not believe that this compromises our conclusions because we were careful to collect leaves of similar ages from a few selected trees for these experiments. There is often greater variation in the chemical composition of leaves within individual species of *Eucalyptus* owing to leaf age and between individual trees than between leaves of the same age from different species (Foley 1987; Foley and Hume 1987*a*). Full details of the chemical composition of the diets used in these experiments were given by Foley and Hume (1987*c*). All experiments were performed from November to February 1983–1984 at Armidale.

After an adaptation period of at least 8 wk, the animals were transferred to metabolism cages in an air-conditioned room (17°–23°C) (Foley and Hume 1987*b*). After a further 3-wk adjustment period, digestible energy (DE) intake was determined by measuring feed intake and total fecal output as described previously (Foley 1987; Foley and Hume 1987*a*). Two greater gliders were killed at each of three times during the day: just before feeding (~1800 hours), during the feeding period (~2300 hours), and after feeding (~0900 hours). Two brushtail possums were killed after feeding, but only one measurement was made at the other two times.

Animals were killed with an overdose of sodium pentabarbitone. The gut was rapidly removed and divided into segments—the forestomach, hindstomach, small intestine (three sections), cecum, proximal colon, distal colon, and rectum. The pH of digesta in these gut segments was measured with narrow-range pH paper. SCFA production rates were measured in the cecum of the greater gliders and separately in the cecum and proximal colon of the brushtail possums. The proximal colon of greater gliders is not enlarged, and therefore no measurement of fermentation rate could be made

in this part of the gut. The contents of the cecum or proximal colon were weighed, immediately mixed, and transferred to glass jars fitted with screw-top lids. After the jars were gassed with CO_2, the digesta were incubated at 37°C for 2.5 h without addition of buffer or substrate.

Samples for SCFA determination were taken from the jars after 0, 15, 30, 60, 90, 120, and 150 min of incubation and transferred to small bottles containing 0.5 mL saturated mercuric chloride solution to stop the fermentation. Incubation jars were gassed with CO_2 after each sampling. In both species, the incubation of cecal contents commenced 4–5 min after death. Sampling from the other parts of the gut proceeded simultaneously.

Field Study

Six free-living greater gliders were shot while feeding in the Styx River State Forest, 65 km east of Armidale. The exact diet could not be determined by analysis of the stomach contents because of the fine particle size and lack of differentiation in the epidermis of different *Eucalyptus* species (W. J. Foley, unpublished). However, on the basis of the preferences of captive animals for the *Eucalyptus* species present in the collection area, the diet probably consisted of young and mature leaves of *E. radiata, E. andrewsii,* and *E. saligna.* The animals were shot between 2055 and 2230 hours and immediately transported to a temporary field laboratory. Here the cecum was removed and SCFA production determined as described above. Samples were stored at 0°C until their arrival at the campus laboratory, where they were held at −20°C until analysis. The maximum interval between death and the commencement of incubation was 20 min.

Analysis

Digesta samples were extracted with distilled water, and the fluid separated by high-speed centrifugation (12,000 *g*) for 15 min. The dry matter (DM) content of each sample was determined by drying a second portion to constant mass at 65°C. Total SCFA was determined by steam distillation (Annison 1954) and titration against NaOH in CO_2-free conditions. The molar proportions of individual SCFA in the distillate were determined by gas-liquid chromatography (Erwin, Marco, and Emery 1961).

Calculations

The production rates of individual and total SCFAs were determined by the zero-time method (Carrol and Hungate 1954) after a first-order regression

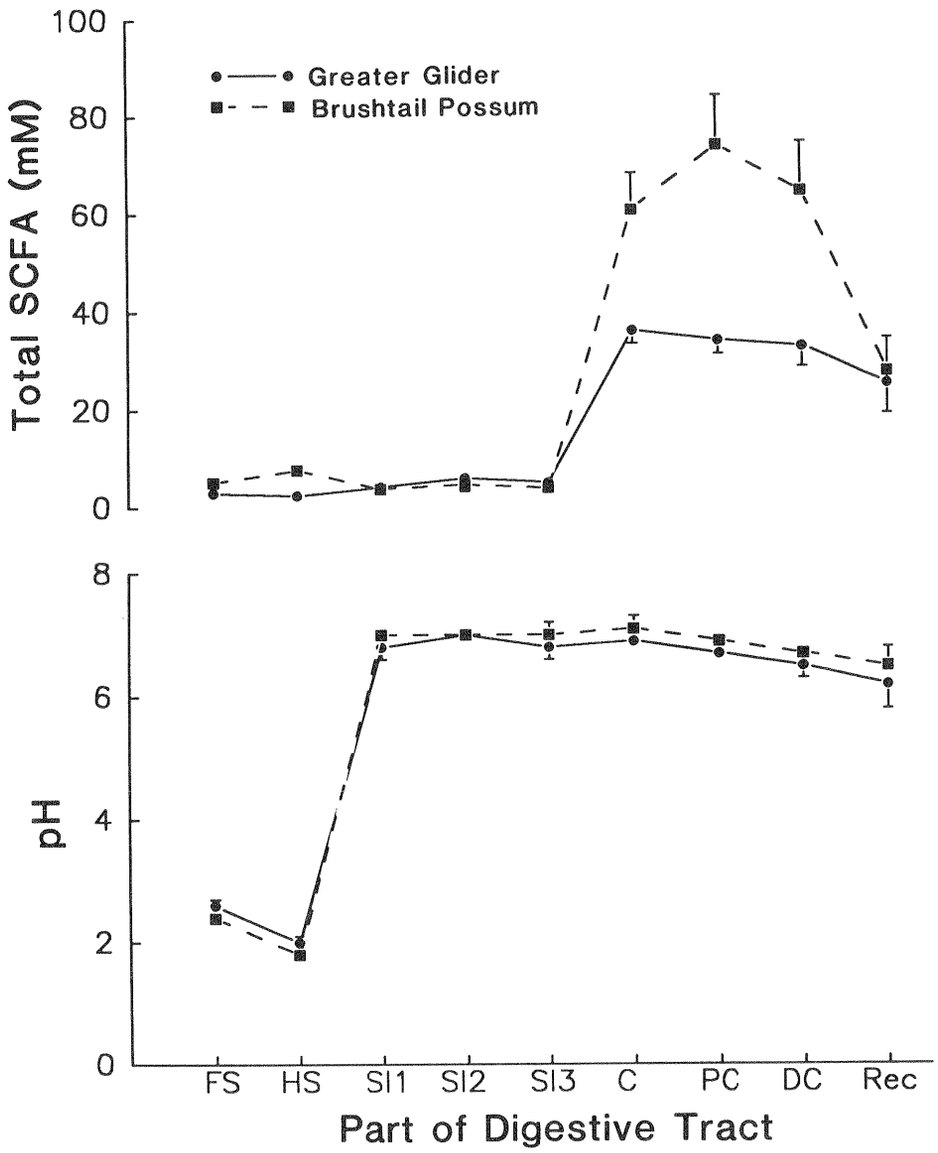

*Fig. 1. Concentration of total short-chain fatty acids (SCFAs) and pH in different parts of the digestive tract of greater gliders (*N = *6) and brushtail possums (*N = *4). Mean ± SE.* FS, *forestomach;* HS, *hindstomach;* SI, *small intestine;* C, *cecum;* PC, *proximal colon;* DC, *distal colon;* Rec, *rectum.*

line was fitted to the data by the least-squares technique. SCFAs were converted to their energy equivalents by means of the calorific values given by Blaxter (1962). Differences between production rates and concentrations of SCFA in different parts of the gut were determined by analysis of variance and *t*-tests (Snedecor and Cochran 1967). Statistical comparisons of concentrations and production rates were not made between the two species or between the captive and field-shot greater gliders, as the diets consumed by each group were, of necessity, different.

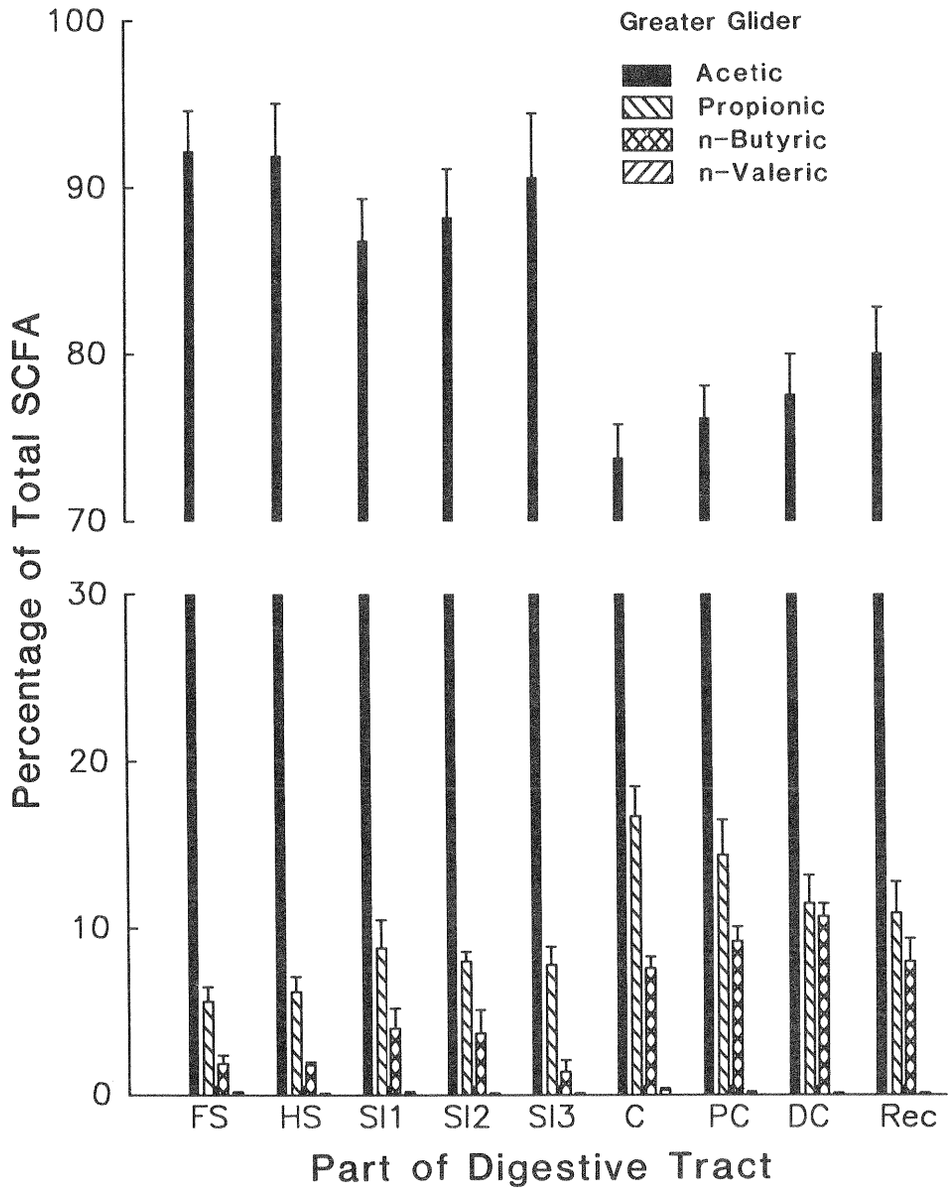

*Fig. 2. Initial molar proportions of individual SCFAs in different parts of the digestive tract of captive greater gliders (*N = *6). Mean ± SE. Abbreviations are as in fig. 1.*

Results

Laboratory Studies in Greater Gliders and Brushtail Possums

Concentration of SCFA in the Gut. The concentration of total SCFA was higher ($P < 0.001$) in the hindgut of both species than in the stomach or small intestine (fig. 1). There was no significant difference ($P > 0.05$) in the concentration of total SCFA between the cecum and proximal colon in either species. Digesta pH was acidic in the stomach but higher ($P < 0.001$) in all other parts of the gut of both species (fig. 1). The molar proportion of acetate was lower ($P < 0.05$) in the hindgut than in the stomach and small

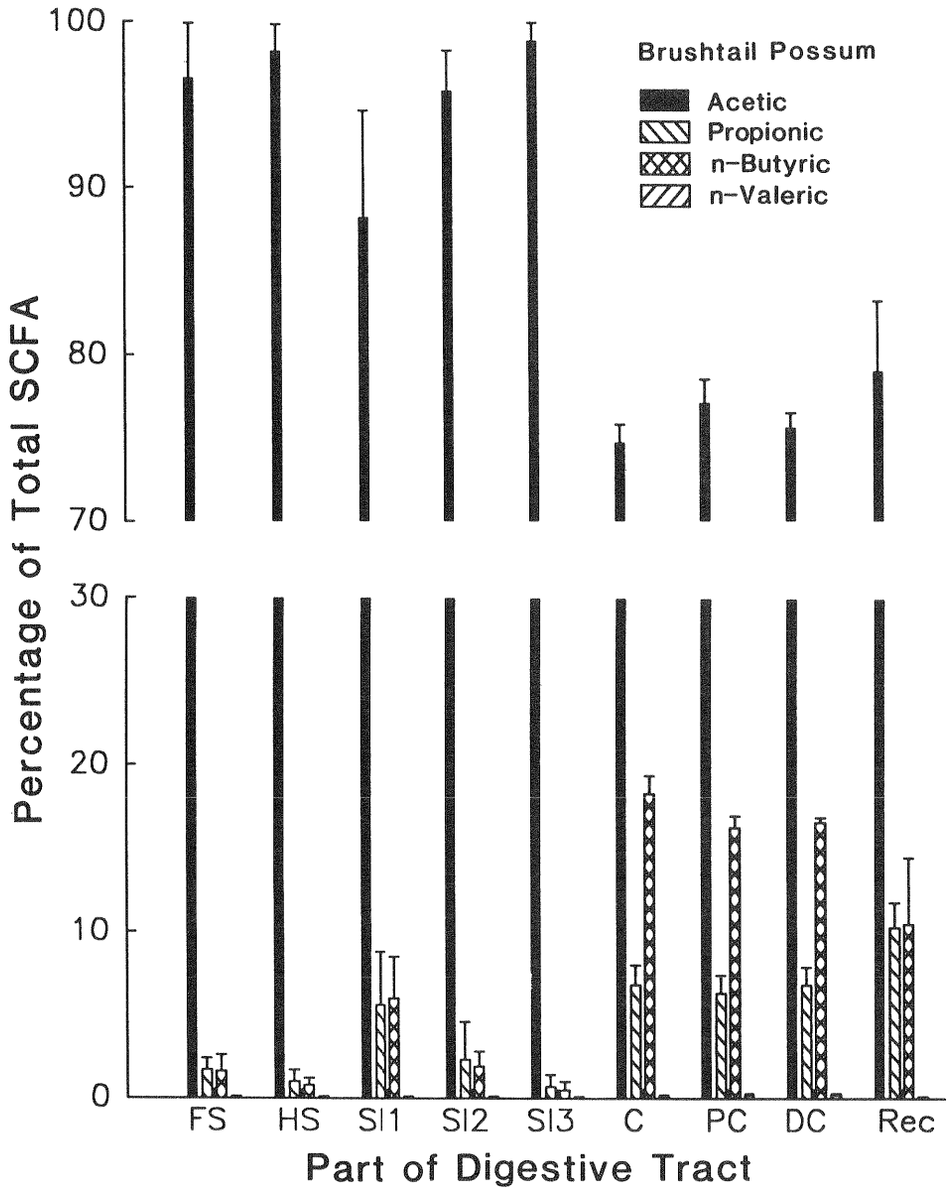

Fig. 3. Initial molar proportions of individual SCFAs in different parts of the digestive tract of brushtail possums (N = *4). Mean ± SE. Abbreviations are as in fig. 1.*

intestine of both species (figs. 2, 3). The proportions of propionate and butyrate showed the opposite trend. In both species n-valeric, isobutyric, and isovaleric acids occurred as only minor constituents of total SCFA (<0.7%).

SCFA Production. In both greater gliders and brushtail possums the concentration of SCFA in hindgut contents changed linearly with increasing incubation time in vitro (fig. 4). This suggested that production of SCFA was not inhibited by the accumulation of the end products of the fermentation and that production rates could be estimated from the slopes of first-order regression lines fitted to the data.

In greater gliders (table 1), the zero-time production rate of propionic

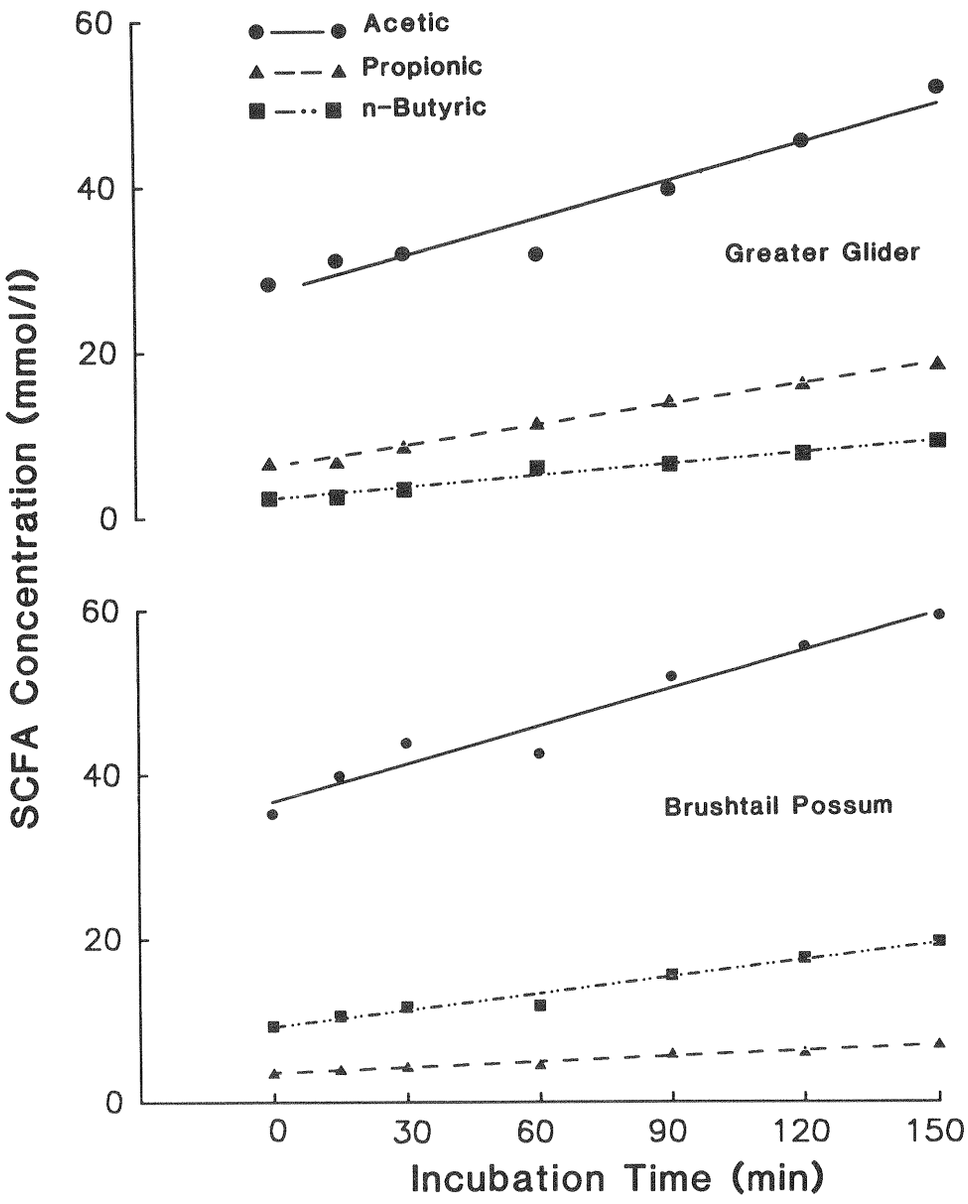

Fig. 4. The change in concentration with time of acetic, propionic, and n-butyric acids in the cecal contents of one greater glider and one brushtail possum during the in vitro incubation of those contents at 37° C.

acid was higher ($P < 0.05$) when the animals were actively feeding than either before or after feeding, but there were no significant differences ($P > 0.05$) in the production of total SCFA throughout the day. The production of acetate (51% of the total SCFA) was lower than the initial molar proportion of acetate in the cecal contents (74%; fig. 2), whereas the propionate and butyrate produced were greater than their initial molar proportions (27% vs. 17% and 20% vs. 7%, respectively). Daily SCFA production (table 1) was calculated by multiplying the production rate of each individual acid by the volume of fluid contained in the hindgut (i.e., total wet weight − [total wet weight × DM%]). There was no difference ($P > 0.05$) in the mean daily SCFA production due to time after feeding. SCFA contributed a mean of 36

TABLE 1

SCFA production rates in captive greater gliders and brushtail possums (individual animal data)

	Greater Glider						Brushtail Possum			
	Killed after Feeding		Killed before Feeding		Killed during Feeding		Killed after Feeding		Killed before Feeding	Killed during Feeding
	1	2	3	4	5	6	1	2	3	4
Body mass (kg)	.97	1.09	1.17	1.19	1.01	1.21	1.68	2.82	2.72	2.06
Contents of cecum (kg)	.10	.11	.14	.12	.07	.08	.13	.12	.19	.11
Contents of proximal colon (kg)							.03	.06	.08	.06
SCFA production (mmol/L/h):										
Acetic:										
Cecum	7.92	6.60	9.00	6.78	10.62	12.90	16.44	13.02	8.94	9.0
Proximal colon							16.02	10.62	14.1	11.52

Propionic:										
Cecum	5.88	4.32	4.86	3.84	8.34	7.80	.97	2.60	1.34	.85
Proximal colon							1.04	1.97	2.15	1.14
Butyric:										
Cecum	5.76	2.88	2.70	1.44	5.52	3.42	5.54	5.11	3.98	2.60
Proximal colon							5.63	4.82	5.58	3.82
Other:[a]										
Cecum	.60	.30	.42	.06	.66	.60	.03	.33	.26	.20
Proximal colon							.17	.16	.61	.20
Daily SCFA production:										
(mmol/d)	36.6	30.8	46.4	28.8	35.5	38.1	81.4	63.9	72.9	83.2
(kJ/kg $^{0.75}$/d)	56.4	40.0	54.5	32.1	50.9	43.3	59.2	38.8	42.2	63.5
% DE intake[b]	9.3	6.6	8.9	5.3	8.3	7.1	17.4	11.4	12.4	18.7

Note. Numbers in column heads denote individual animals.
[a] n-Valeric, isobutyric, and isovaleric acids.
[b] From Foley (1987) and Foley and Hume (1987*a*).

mmol/d or 46 kJ/kg$^{0.75}$/d. This was 7.3% of the mean DE intake of the animals (610 kJ/kg$^{0.75}$/d) previously determined by Foley (1987).

There were no significant differences ($P > 0.05$) in the production rates of SCFA between the cecum and the proximal colon in the brushtail possum. Acetate was the principal SCFA produced (67% of total; table 1) but in contrast to the pattern observed in greater gliders, butyrate constituted a greater proportion of the total SCFA produced (25%) than did propionate (8%). As in the greater gliders, the production rate of acetate was lower, and that of propionate and butyrate higher, than initial molar proportions of these three acids in both the cecum and proximal colon. The ratio of proportional production rates to the initial molar proportions were 0.9, 1.2, and 1.5 for acetate, propionate and butyrate, respectively.

The total daily production of SCFA was higher ($P < 0.05$) in the cecum of the brushtail possum than in the proximal colon, which reflected the larger volume of digesta contained in the cecum (table 1). SCFA contributed a mean of 75.4 mmol/d or 51 kJ/kg$^{0.75}$/d. This was 15% of mean DE intake (340 kJ/kg$^{0.75}$/d; Foley and Hume 1987*a*).

Field Study of Greater Gliders

There were no significant differences in the molar proportions or SCFA production rates related to the time at which animals were shot. In the field study, all six samples covered the period when the animals were actively feeding. The initial cecal SCFA concentrations (70 mM: table 2) were twice as high as those recorded in the laboratory study. There were also differences in the molar percentages of individual SCFAs compared with those in the laboratory study. In particular, the proportion of acetate was lower (63% vs. 74%), and of propionate (22% vs. 17%) and butyrate (13% vs. 7%) higher. Although SCFA productions were lower than those recorded in the laboratory study, this was offset by a greater volume of digesta contained in the cecum per unit body mass (11.9% vs. 9.5%), so that daily production of SCFA was greater but the caloric equivalent per unit metabolic body mass was similar to that measured in the laboratory (table 2).

Discussion

The concentrations of total SCFA in the hindgut of both the greater glider and the brushtail possum confirmed anatomical and microscopic evidence that the hindgut was the principal site of microbial activity in both species.

TABLE 2

SCFA concentration, molar proportions, and SCFA production rate in the cecum of greater gliders in the field

	Animal						
	1	2	3	4	5	6	Mean ± SE
Time of death (h)	2055	2105	2120	2130	2215	2230	
Body mass (kg)	1.22	1.20	1.22	1.29	1.33	1.15	1.24 ± .03
Contents of cecum (kg)	.14	.15	.15	.15	.15	.15	.15 ± .002
Total SCFA (mM)	66.4	56.8	82.8	56.8	69.9	86.4	69.9 ± 5.1
Initial SCFA molar proportions (%):							
Acetic	64.3	64.4	60.2	58.4	60.4	69.6	62.9 ± 1.7
Propionic	22.2	23.8	21.8	25.1	22.7	17.2	22.1 ± 1.1
Isobutyric	.2	.8	.4	.6	.8	.2	.5 ± .1
n-Butyric	11.3	9.8	16.6	13.4	13.2	12.5	12.8 ± .9
Isovaleric	1.5	.9	1.0	1.9	1.7	.5	1.3 ± .2
n-Valeric	.6	.4	.1	.6	1.1	.1	.5 ± .2
Production of SCFA:							
(mmol/L/h)	19.8	19.2	13.2	15.0	18.6	20.4	17.7 ± 1.2
(mmol/d)	53.2	55.8	37.7	42.5	51.3	61.7	50.4 ± 3.6
(kJ/kg $^{0.75}$/d)	55.5	59.1	39.3	42.5	50.3	67.5	52.4 ± 4.3

However, the concentration of SCFA in the cecum of the greater glider in our laboratory study was only half that in the greater gliders shot in the field and half that in the brushtail possums. Most mammals maintain concentrations of SCFA of around 100 mM in the hindgut, regardless of their diet or type of digestive system (Engelhardt and Rechkemmer 1983). One exception is the koala (Cork and Hume 1983), in which SCFA concentrations in the hindgut were similar to those we observed here in the captive greater glider. Some studies of rabbits have measured cecal SCFA concentrations of only 50 mM (Hoover and Heitman 1972), but other studies of wild rabbits have found amounts of as much as 115 mM (Henning and Hird 1972*a*). SCFA concentration at any time reflects the balance between production and absorption. Cork and Hume (1983), on the basis of studies of SCFA absorption in eutherian mammals, suggested that the low SCFA concentrations in the hindgut of the koala were more likely to be due to a slow rate of production than to rapid absorption. Recent work on SCFA absorption in the greater glider and brushtail possum confirms this suggestion (Rübsamen et al. 1983); SCFA were rapidly absorbed from the hindgut of both species, although there were differences in the rate of absorption in different parts of the hindgut. In view of these data, the relatively low concentrations of SCFA in the hindgut of marsupials that feed on *Eucalyptus* leaves probably reflects the low production rate due to a poorly fermentable diet.

However, SCFA are the major anions in the hindgut and so play an important role in absorptive and secretory processes. Both greater gliders and rabbits (and the koala but not brushtail possums; Bjornhag 1972; Cork and Warner 1983; Foley and Hume 1987*b*) selectively retain fine particulate digesta in the cecum. Greater gliders and rabbits also show a similar pattern of water and electrolyte flux in the hindgut (Clauss 1978; Rübsamen et al. 1983). These two aspects of hindgut function are thought to be related (Bjornhag 1981). Although diet probably exerts the major effect on cecal SCFA concentration, the low concentration of SCFA in the greater glider and koala may also be related to the particular pattern of water and ionic flux across the hindgut that seems necessary to maintain the mechanism of fine particle retention in the hindgut.

SCFA production rates in the hindgut of both captive and wild-shot greater gliders and the brushtail possum were similar, but almost twice those measured by Cork and Hume (1983) in the koala. Few studies of comparable eutherian mammals have been reported. Milton and McBee (1983) reported very rapid fermentation rates (up to 250 mmol/L/h) in the cecum of the howler monkey (*Alouatta palliata*). This may have been because some of the sugars from the diet of fruit pulp and young leaves reached the hindgut.

However, such rapid rates of production are unexpected, considering the high initial molar proportion of acetate in the cecum (94%) as well as the relatively slow turnover of cecal contents in this species (Milton 1981).

The greater initial proportion of acetate in the hindgut of the brushtail possum compared with that of the greater glider suggests that the brushtails were fermenting a higher-fiber substrate or, alternatively, a lower fermentable component of the diet. Although the *Eucalyptus* species fed to these animals were different, the fiber contents of the diets were comparable (Foley and Hume 1987*c*). However, unlike the koala and greater glider, the brushtail possum does not selectively retain fine particulate digesta, so the substrate fermented in the hindgut may be potentially less fermentable than in the other species. The higher proportion of acetate to propionate in the captive compared with the wild-shot greater gliders may also result from the fermentation of substrates of different fermentability. This probably is due to the selection of a higher proportion of young leaves in the diet of greater gliders in the field.

Nonetheless, in both groups of greater gliders and in the brushtail possums the proportional contributions of the three major fatty acids to total SCFA production differed from their pattern of initial concentration. This difference was expected in view of earlier observations (Rübsamen et al. 1983) that SCFA were absorbed in direct proportion to their chain length in both species. It is unlikely that this pattern resulted from the end-product inhibition of acetate production, since the production of acetate was slow and linear in all cases (fig. 4).

From a knowledge of the concentration of SCFA in the feces and the fecal DM excretion in both species (Foley 1987; Foley and Hume 1987*a*), we calculate that 98%–99% of the SCFA produced was absorbed in both greater gliders and brushtail possums. Although production rate of SCFA was similar in the two species, this absorbed SCFA contributed 7% of the mean intake of DE of greater gliders but 15% of that of the brushtail possums. This difference was principally due to the lower DE intakes of the brushtails, although the greater proportion of butyrate produced in the brushtails also increased the caloric value of absorbed SCFA. Although the preferential absorption of butyrate may benefit the animal by virtue of its higher energetic value, there is still uncertainty about the extent of metabolism of butyrate in the gut wall (Henning and Hird 1972*b;* Roediger 1980; Woodnutt and Parker 1980).

The relatively low fermentation rate in *Eucalyptus*-feeding marsupials is likely due to the highly lignified nature of *Eucalyptus* cell walls (Cork and Hume 1983; O'Brien, Lomdahl, and Sanson 1986; Foley 1987; Foley and Hume 1987*a*) and the inhibitory effects of plant polyphenolics, at least in

the brushtail possum (Foley and Hume 1987*a*). Low fermentation rates are also consistent with the low digestibilities of cell walls reported for *Eucalyptus* diets. However, it is unlikely that cell walls were the sole substrate fermented in the hindgut. Greater gliders digested a mean of 2.9 g cellulose/d (Foley 1987), and brushtail possums 1.7 g (Foley and Hume 1987*a*). If it is assumed that the caloric density of cellulose is 16.8 kJ/g and that the efficiency of conversion of carbohydrate to SCFA in these marsupials is similar to that found in ruminants (i.e., 70%–75%; Agricultural Research Council 1980), then 25% of SCFA production in greater gliders and 58% in brushtail possums must have arisen from the fermentation of substrates other than cellulose. Other cell wall constituents such as hemicelluloses and pectins are the most likely substrates, but intestinal mucoproteins (Vercellotti, Salyers, and Wilkins 1978) and glucuronides excreted in the bile may also be important.

Regardless of the contribution of SCFAs to energy requirements of these animals, their major importance may lie elsewhere. Water absorption depends on the creation of an osmotic gradient generated by the active transport of sodium and SCFA (Stevens 1978). Interrelationships between sodium, SCFA, and water absorption have been demonstrated in the hindgut of several species (see, e.g., Argenzio, Miller, and Engelhardt 1975; Argenzio and Whipp 1979; Umesaki et al. 1979). Although Rübsamen et al.'s (1983) results with greater gliders and brushtail possums were inconclusive on this point, this may have been due to differences in the buffering capacity of the solutions used in that study. At present there are insufficient data to judge whether the reabsorption of water and electrolytes or the "detanning" of tannin-protein complexes (O'Brien et al. 1986) are of sufficient importance to account for the development of the large ceca found in arboreal marsupials. However, in the case of the koala, Cork and Sanson (1989) have pointed out the apparent anomaly between a digestive system that is geared to the production (by mastication) and selective retention of fine digesta particles in the hindgut and the apparent minor contribution of hindgut fermentation to the animal's energy intake. A similar argument could apply to the current data on greater gliders.

Although in vitro estimates of SCFA production are usually regarded as being underestimates of in vivo rates, the amount of SCFA produced in this study and that of Cork and Hume (1983) accounts for the cell wall constituents digested. We would thus argue that unless significant amounts of soluble carbohydrates escape digestion in the stomach and small intestine, which seems unlikely, our estimates in vitro reasonably reflect production rates in vivo on these particular diets. We suggest that in future more atten-

tion be paid to studies on the release and digestion of cell contents, because these contribute the bulk of the energy requirements for this group of animals.

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