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## Viscoelastic behaviour aids extrusion from and reabsorption of the liquid phase into the digesta plug: creep rheometry of hindgut digesta in the common brushtail possum *Trichosurus vulpecula*

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**Abstract** Temporal variation in the rheometric properties of the proximal and distal colonic digesta of an arboreal marsupial folivore, the common brushtail possum, was examined to assess flow behaviour during peristalsis, segmentation and other aspects of intestinal motility. The time-dependent rheometric characteristics on application of a constant shear stress within the physiological range showed an initial elastic and subsequent viscoelastic phase, which fitted Burger's model of creep compliance. Similarly, the time-dependent rheometric characteristics on recovery from shear stress fitted with a generalised two-component Maxwell model of elastic and viscoelastic components for creep recovery. Differences in the relative magnitudes of the viscoelastic components during recovery from those during shear indicated that the physical properties of the digesta plug changed with sustained shear stress, a phenomenon, which is likely to result from extrusion of the liquid phase from the solid elements of the digesta plug. There was significant viscoelastic recovery during the initial 4 s following cessation of stress, which would allow for prompt concomitant reabsorption of the liquid phase into the digesta plug. This supports a hypothesis of alternate extrusion and reabsorption of the liquid phase of the digesta plug. This would promote both nutrient absorption across the intestinal wall (from liquid extrusion) and enzyme permeation and digestion (from liquid absorption into the plug). However, the presence of a slower component of viscoelastic recovery indicates

that liquid phase reabsorption into the digesta plug is incomplete if the interval before a subsequent contraction is less than 150 s, in which case unreabsorbed liquid may be driven either orally or aborally. This would at least partly account for differences in retention times of liquid and solid phase digesta markers reported for the gastrointestinal tracts of numerous vertebrate species.

### Introduction

Recent work has indicated that the digesta of a hindgut fermenting herbivore, the common brushtail possum (*Trichosurus vulpecula*), has high and non-Newtonian viscosity, which would cause it to exhibit laminar flow under the physiological conditions associated with peristalsis (Lentle et al. 2005). It is also likely that the local compression of a plug of digesta during peristalsis would express liquid from the solid phase matrix. Although these phenomena may account for the local transfer of the soluble products of digestion to the mucosa, the extent to which any expressed liquid and secreted enzymes are subsequently reabsorbed into the solid matrix of digesta depends on the ability of the solid elements to retain their elastic properties and to re-expand following peristaltic compression. The extent of such re-expansion depends upon the balance between the viscous and the elastic properties, i.e. the extent to which stress resulting from intestinal contraction can be stored as elastic energy over time (the elastic storage modulus,  $G'$ ) and the extent to which such stress is dissipated by flow (the loss modulus,  $G''$ ).

Digesta flows through the lumen of the gut from sites of radial constriction to adjacent sites of dilatation, where the pressure is relatively reduced (Davenport 1977; Macagno and Christensen 1981; Jeffrey et al. 2003). Any axial displacement of digesta by radial contraction is opposed by friction from the walls of the gut and between the concentric layers of the digesta. Thus, peristaltic contractions cause shear stress to propagate

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inwards from the wall (Lentle et al. 2002) across the viscous and pseudoplastic (Lentle et al. 2005) contents of the lumen. The presence of shear stress between the outermost adjacent concentric layers of fluid leads to the lowering of viscosity and the establishment of laminar flow around the periphery of a centrally moving plug of digesta (Lentle et al. 2002, 2005).

To study the behaviour of digesta in physiologically relevant terms, it is necessary to examine its rheological properties under shear stress rather than under compressive or tensional stress. This is not to say that digesta does not on occasion undergo direct compression or tension. Axial tension or compression may result from gravitational forces acting on vertically oriented contiguous columns of digesta (Arun 2004). However, static contiguous columns of digesta do not commonly occur and thus it is likely that the majority of forces acting on digesta are those of shear stress.

Although Lentle et al. (2005) showed that extrusion of the liquid phase occurs when digesta undergo direct hydraulic compression within the physiological range of pressures, they did not show that similar extrusion occurred in shear stress, i.e. that liquid may be extruded from the digesta during laminar flow. Dynamic rheometry (Lentle et al. 2005) has confirmed that digesta have a significant elastic storage modulus ( $G'$ ) and that this is consistently greater than the loss modulus ( $G''$ ) during successive cyclic applications of shear stress in a range of frequencies (0.01–10 Hz). This indicates that digesta exhibit elastic recovery over a range of contraction frequencies. However, it is also important to describe the relationship between elastic and flow behaviour, i.e. variation in  $G'$  and  $G''$  (Steffe 1996) over time, as the rate of flow and consequent loss of stored elastic energy in digesta during and following peristalsis or segmentation will influence the extent to which the elastic components are able to re-expand between successive contractions. This will determine the extent to which liquid and enzymatic secretions are reabsorbed into the digesta plug following extrusion. The temporal relationship between  $G'$  and  $G''$  is also important as it may influence the speed of propagation of these contractions. Thus, the degree to which tension is generated in the walls of the contracting segment from resistance of contained digesta to flow (Larson and Schultze 2002) and the extent to which the walls adjacent to the zone of contraction are distended by extruded fluid are likely to influence the extent to which the tone-dependent (Smith et al. 2003) and tone-independent (Spencer et al. 2002) intrinsic stretch receptors that govern the propagation of peristalsis are activated.

The current study provides a baseline for future comparisons by determining the timing and extent of elastic compression and recovery of the solid phase in the digesta of relatively uniform particle size composition from a simple tubular component of the gut. It also tests whether the application and relaxation of shear stress from peristalsis causes liquid to be extruded from, and subsequently reabsorbed into the solid phase of

digesta, and the extent to which such extrusion and reabsorption change during passage through a tubular gut component.

The colon of the common brushtail possum *T. vulpecula* is a simple non-hausted cylinder (Snipes and Carrick 2003) and does not selectively retain either particulate (Wellard and Hume 1981) or liquid phases of the digesta (Sakaguchi and Hume 1990). The principal physical change in the digesta during its passage through this structure is a reduction in water content (Lentle et al. 2005). In this paper, we determined the particle size composition, water content, creep compliance and creep recovery of digesta from the proximal and distal colon of common brushtail possums that had been grazing on pasture.

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## Materials and methods

### Digesta sampling

Fresh digesta were obtained from the proximal and distal halves of the colon of ten male common brushtail possums that were shot whilst grazing on a single night during local pest control operations. The abdomen was opened immediately after death, the entire gastrointestinal tract was removed, the colon was ligated at its midpoint and the contents of the proximal and distal halves of the colon were collected into separate containers. The samples were bulked from the ten animals and stirred with a spatula for 5 min. This technique was used to avoid inadvertent additional fragmentation of the solid phase of the digesta. The mixed samples were chilled at 4°C pending rheometric analysis, which was conducted within 24 h.

The digesta from the proximal and distal colon of a further three similarly treated male possums were removed and frozen separately pending determination of dry matter content and particle size distribution.

### Rheological measurements

#### Background

Creep rheometry describes the behaviour of a material over time during (creep-compliance) and following (creep-recovery) the application of a constant (shear) stress.

The application of stress may cause the material to undergo elastic deformation or to flow. Thus, at any moment, the total stress ( $\sigma_{\text{tot}}$ ) induced by the constant strain can be considered as the sum of these two effects (Steffe 1996).

$$\sigma_{\text{tot}} = \sigma_{\text{elastic}} + \sigma_{\text{viscous}}, \quad (1)$$

$$\sigma_{\text{tot}} = G\gamma + \mu \frac{\delta\gamma}{\delta t} \quad (2)$$

given that, in viscous flow,  $\sigma_{\text{viscous}} = \mu \frac{\partial \gamma}{\partial t}$  with  $\mu$  the viscosity and  $\frac{\partial \gamma}{\partial t}$  the shear rate, and that, in a Hookean elastic solid (i.e. one which is perfectly elastic),  $\sigma_{\text{elastic}} = G\gamma$ .

The arithmetic relationship between elastic and viscous stress is determined by the manner in which the solid and liquid components interact with each other and may vary with the composition of these two components. This is best conceptualised using arrangements of model elements that convey either elastic deformation or viscous flow. Elastic deformation can be portrayed as a simple spring, while viscous flow can be portrayed by a 'dashpot', a device in which application of force via a shaft causes the fluid to be driven through a small hole in a piston. A dashpot and a spring can be mounted in series (the Maxwell element in the Maxwell model) (see Fig. 2), so that applied stress is initially taken up by elastic extension and subsequently ameliorated by viscous flow. Alternatively, a spring and dashpot may be mounted in parallel (the Kelvin element in the Burgers model) (see Fig. 1), where elastic extension is limited by viscous flow (i.e. some initial viscous flow is required to enable elastic extension).

Different dispositions of these elastic and viscous elements can be used to model differing patterns of response to the sudden application of stress or strain. Several models are possible using more than one of each

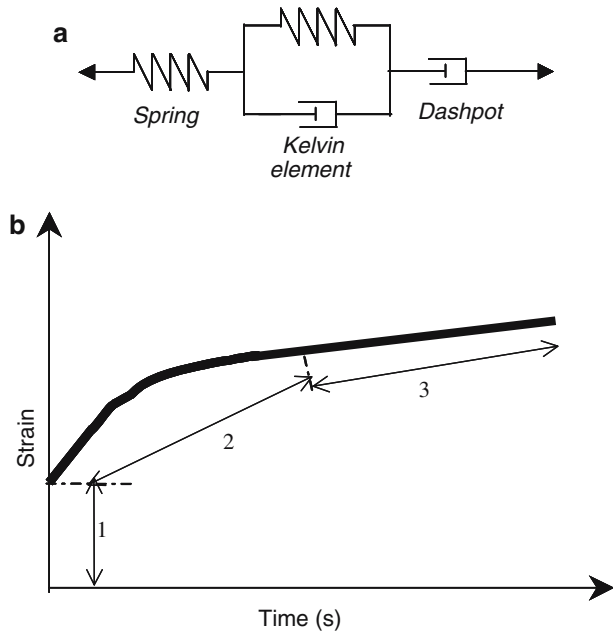
component to produce different overall patterns of response. In exploring the creep/recovery characteristics of a particular material, a variety of such models may be statistically evaluated for best fit to the empirical data. The identification of a well-fitting model allows for a mechanistic explanation of the dynamic behaviour of the material. Similar models may be devised to describe the changes following relaxation of constant stress or strain when residual stored elastic energy is released and the pattern of recovery generated by a particular model tested for fit against the relaxation portion of the creep curve of a particular material.

### Sampling and procedure

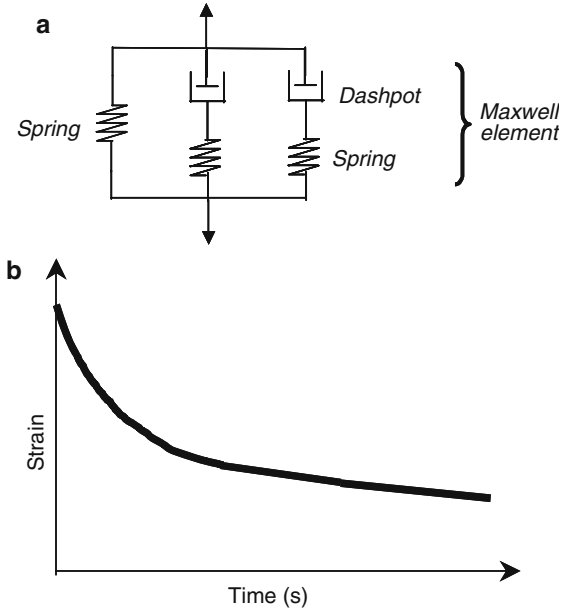
Rheometric analyses and particle size analyses were conducted on three sub-samples from each of the pooled digesta samples of both the proximal and distal colon. Pooling was necessary to obtain sufficient volume of digesta to conduct these analyses.

### Rheometry

The creep-recovery curves of proximal and distal colonic digesta were determined at 23°C using a Rheometrics SR500 controlled-stress rheometer, with a plate-plate



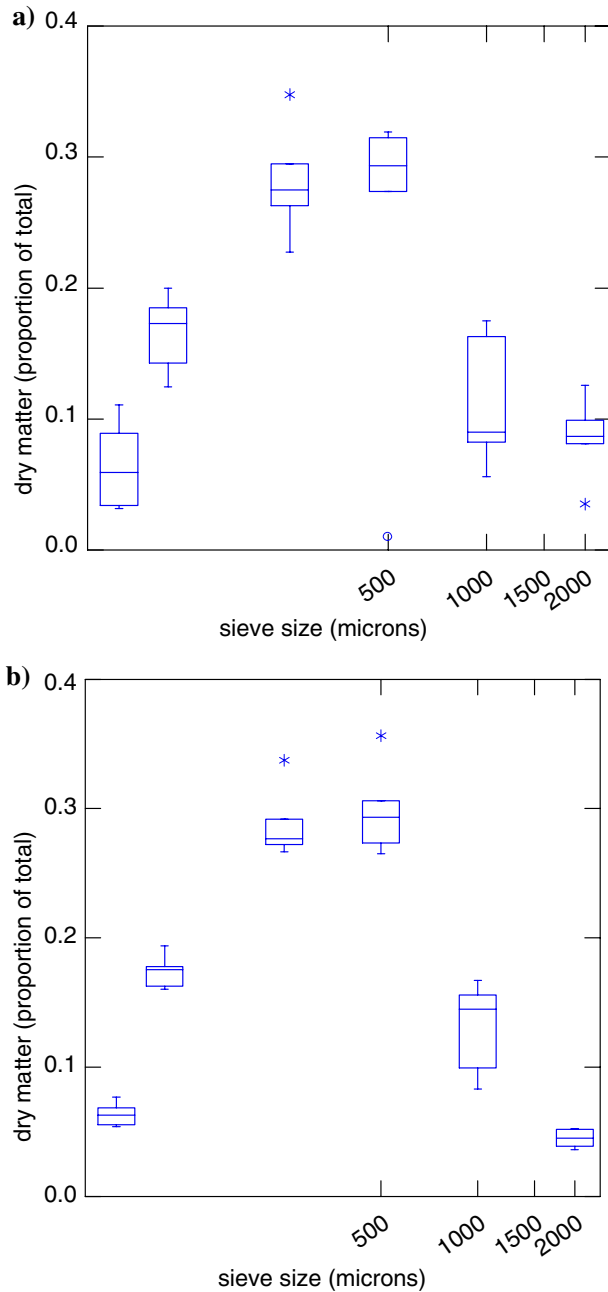
**Fig. 1** Rationale of the Burgers model used in the analysis of creep-compliance of colonic digesta of common brushtail possums. **a** Mechanical analogues of terms incorporated in the model are, on the left, an elastic element represented by a spring; on the right, a viscous flow element represented by a free dashpot; in the centre a Kelvin element of an elastic spring and dashpot in parallel. **b** Typical creep-compliance curve of the Burgers model showing an initial elastic response (the intercept with the ordinate) (1); a retarded elastic behaviour from the Kelvin element (represented by the curvilinear portion of the graph) (2), where elastic energy stored in the spring is dissipated with time by flow within the dashpot; and viscous Newtonian flow from the free dashpot at longer times (3)



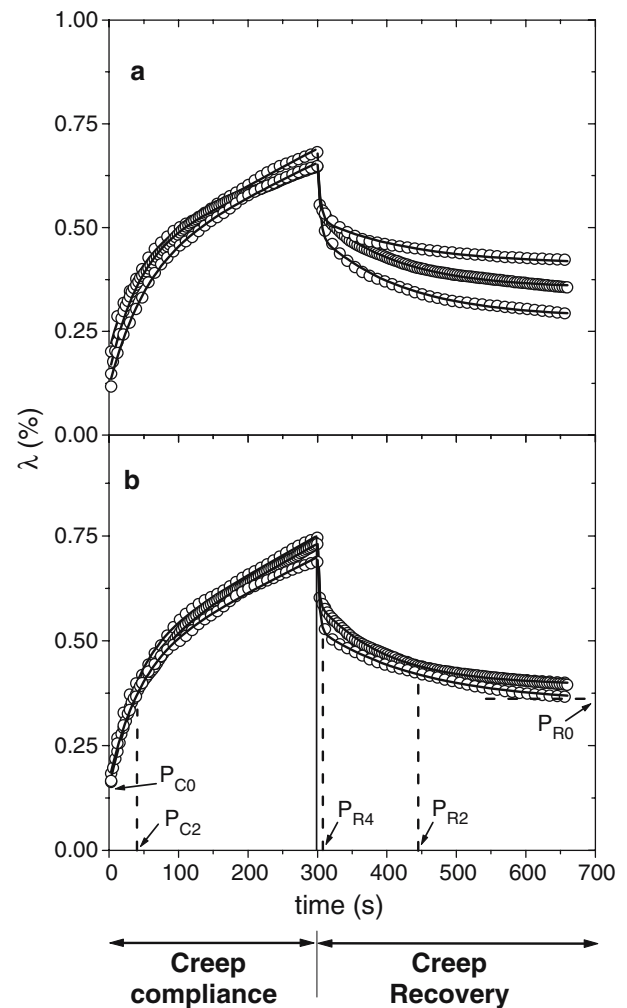
**Fig. 2** Rationale of the Maxwell model used for the analysis of relaxation characteristics (*creep-recovery*) of colonic digesta of common brushtail possums. **a** Mechanical analogues of terms incorporated in the model comprising an elastic element represented by a spring (*on the left*) in parallel with two Maxwell elements (each a spring and dashpot in series). **b** Typical creep-recovery curve of the model. There is retarded recovery governed by the two Maxwell elements that yields an initial steep, then a less steep, curvilinear decay

geometry, a rotating plate diameter of 40 mm and a plate–plate a gap of 5 mm. The large plate gap was necessary as particle sizes were of the order of 500  $\mu\text{m}$ . The large diameter plate caused the shear to be distributed though a sample which was largely occluded by the plate and limited extrusion of the liquid phase to the periphery of the digesta sample. This approach, in

conjunction with the low-strain force applied, limited extrusion of the fluid to a low volume at the periphery of the plate, a position from which it was readily reabsorbed on cessation of applied strain. Creep data were recorded following the instantaneous application of a constant stress of 15 Pa (or 1.5 mm water at 4°C) for 300 s. The magnitude of the applied stress was within the viscoelastic region of an initial exploratory frequency stress-sweep analysis, and within the range of physiological pressures exerted by peristaltic and other types of contraction (Hightower 1968; Connell 1968). Rheometric data were recorded during recovery for 300 s following the termination of the applied stress. The duration of the creep phase was chosen on the basis that it exceeded the duration of most types of colonic contraction. The duration of recording of the recovery phase on the basis that it exceeded the longest reported interval between successive colonic contractions, which is in humans (Connell 1968).



**Fig. 3** Box plots of the particle size distributions of digesta from the proximal (a) and distal (b) halves of the colon from three randomly selected adult male possums shot whilst grazing on farmland. Each *data point* represents the pooled results of two replicates from each of the three possums. The results are expressed as dry matter retained by each sieve as a proportion of total particulate matter retained by the sieves. Sieve mesh sizes were 2, 1 mm, 500, 250, 106 and 75  $\mu\text{m}$



**Fig. 4** Creep-compliance and recovery curves represented as the variation of strain  $\lambda$  with time of replicated samples of pooled and mixed digesta from the proximal (a) and distal colon (b) of brushtail possums. Dashed lines correspond to calculated retardation and relaxation times (see text for detail of parameters)

Curves were fitted to the creep-recovery data using a least squares fitting procedure in Origin Microcal software. The following Burgers model describing strain resulting from the continuous application of external shear was fitted to the creep data:

$$\gamma_C(t) = P_{C0} + P_{C1}(1 - \exp(-t/P_{C2})) + t/P_{C3}, \quad (3)$$

where  $\gamma_C$  is the shear strain resulting from the creep measurement,  $t$  is time after initial application of the stress,  $P_{C0}$  is the instantaneous strain,  $P_{C1}$  and  $P_{C2}$  are the delayed strain and the retardation time of the Kelvin element of the Burgers model, respectively, and  $P_{C3}$  is an equivalent of the Newtonian viscosity ( $P_{C3} = \mu/\sigma_0$ , where ( $\mu$  is the Newtonian viscosity and  $\sigma_0$  the applied stress), which can be derived from the slope of the creep-compliance curve taken at a time that is sufficiently long to exceed the period during which the Kelvin element is in operation. The elastic and viscous contributions of the parameters in this model are represented graphically in Fig. 1 (Steffe 1996).

The recovery curve was fitted using a two-element generalised Maxwell model (Fig. 2), describing recovery driven by intrinsically stored energy following the cessation of applied stress:

$$\gamma_R(t) = P_{R0} + P_{R1} \exp(-t/P_{R2}) + P_{R3} \exp(-t/P_{R4}), \quad (4)$$

where  $\gamma_R$  is the shear strain resulting from the recovery measurement, where  $P_{R0}$ ,  $P_{R1}$  and  $P_{R3}$  are delayed strain constants and  $P_{R2}$  and  $P_{R4}$  are relaxation times. The elastic and viscous contributions of the parameters in this model are represented graphically in Fig. 2 (Steffe 1996).

#### Determination of particle size and dry matter content

Particle size spectra were determined by wet sieving (Waghorn 1986). Two paired aliquots of frozen digesta were weighed and assigned randomly to two treatments. The first pair was oven-dried at 80°C in a forced draft oven for 3 days to determine the dry matter content. The second pair was filtered through a nest of sieves (Endecott, London, UK) of mesh size 2, 1 mm, 500, 250, 106 and 75  $\mu\text{m}$ . The material retained on each of the sieves was washed onto a dry, pre-weighed filter paper. The

filter papers were dried for 3 days in a forced-draft oven at 80°C before re-weighing.

The masses of particles retained by each sieve were expressed as a percentage of the total mass of retained particulate matter.

#### Statistical analysis

Statistical comparisons of durations of creep and recovery components were conducted in SYSTAT by repeated measures ANOVA (Wilkinson 1990).

## Results and discussion

The particle size distributions did not differ significantly between digesta from the proximal and distal halves of the colon (Fig. 3). The material retained on the coarse sieves (size >1 mm) consisted mainly of fragmented grass with a small number of seeds. The seeds were removed prior to rheometric analysis. The proportion of dry matter in the proximal colonic digesta ( $0.063 \pm 0.003$ ) was significantly lower (df 1,10, 17.7,  $P=0.002$ ) than that in the distal digesta ( $0.122 \pm 0.014$ ).

In the following discussion, the rheological behaviour of the digesta will be described first and the physiological implications will be considered subsequently.

The creep-compliance and creep-recovery of pooled digesta from the proximal (Fig. 4a) and distal colon (Fig. 4b) varied between samples, but the overall pattern of responses was similar. This variation was likely a consequence of minor inhomogeneities in the digesta as, in order to prevent artifactual fragmentation of the solid phase, extensive mixing had not been performed. When the experimental data were fitted by Eqs. 3 and 4 (Table 1),  $R^2$  (observed versus predicted) was greater than 0.99 in all cases. As the constants derived from the fitting of these curves did not differ significantly, the results from both the proximal and distal colonic digesta were pooled.

The results from the pooled creep-compliance measurements showed that, immediately following the application of stress, the digesta had an initial elastic

**Table 1** Values of rheological parameters for the creep-compliance and recovery of three successive sub-samples of pooled proximal and pooled distal colonic digesta from ten common brushtail possums ( $P_{C0}$ - $P_{C3}$ ) ( $P_{R0}$ - $P_{R4}$ )\*

Creep	Recovery								
	$P_{C0}$ (%)	$P_{C1}$ (%)	$P_{C2}$ (s)	$P_{C3}$ (s)	$P_{R0}$ (%)	$P_{R1}$ (%)	$P_{R2}$ (s)	$P_{R3}$ (%)	$P_{R4}$ (s)
Proximal colon 1	0.20 ± 0	0.220 ± 0.013	36.8 ± 4.2	1,116 ± 70.7	0.283 ± 0.002	0.200 ± 0.003	123.03 ± 5.11	0.195 ± 0.006	3.55 ± 0.28
Proximal colon 2	0.15 ± 0	0.302 ± 0.012	42.5 ± 3.0	1,498 ± 114.4	0.354 ± 0.001	0.183 ± 0.001	109.97 ± 2.16	0.109 ± 0.003	2.80 ± 0.20
Proximal colon 3	0.12 ± 0	0.302 ± 0.013	52.8 ± 3.3	1,261 ± 81.4	0.412 ± 0.002	0.108 ± 0.002	133.91 ± 8.35	0.131 ± 0.005	4.47 ± 0.36
Distal colon 1	0.16 ± 0	0.310 ± 0.01	37.5 ± 2.5	1,071 ± 54.2	0.398 ± 0.001	0.193 ± 0.001	92.62 ± 1.34	0.155 ± 0.003	1.83 ± 0.11
Distal colon 2	0.15 ± 0	0.310 ± 0.01	44.7 ± 3.1	1,107 ± 64.8	0.395 ± 0.001	0.195 ± 0.001	98.66 ± 1.46	0.141 ± 0.003	1.97 ± 0.13
Distal colon 3	0.17 ± 0	0.283 ± 0.013	42.8 ± 3.5	1,194 ± 80.3	0.352 ± 0.002	0.174 ± 0.001	151.89 ± 4.51	0.165 ± 0.003	2.98 ± 0.16
Mean	0.158	0.288	42.74	1,208	0.366	0.176	118.35	0.149	2.93

\*These were obtained by fitting the experimental data to a four-element Burgers model of creep-compliance and a two-element generalised Maxwell model of creep-recovery

strain ( $P_{C0}$ ) of 0.16% deformation (range 0.12–0.20%). The degree of strain subsequently increased in a non-linear fashion with time, in a manner corresponding to the Kelvin element in Burgers model (Fig. 2). The amplitude of this delayed strain ( $P_{C1}$ ) and its retardation time constant ( $P_{C2}$ ), i.e. the time of maximal effect from this component, were 0.29% deformation and 42.7 s, respectively (see broken lines in Fig. 4). At times in excess of 150 s, the strain increased linearly with time with mean equivalent Newtonian viscosity ( $P_{C3}$ ) of 1,208 s (Table 1) which, with an applied constant stress of ( $\sigma_0$ ) 15 Pa, gives a Newtonian viscosity of  $\sim 18,000$  Pa s. This value lies in the reported range of the apparent viscosity of bulked common brushtail possum colonic digesta determined at low-shear rates by rotational viscometry (Lentle et al. 2005).

The results from the pooled creep-recovery data showed that strain decreased immediately on removal of the applied stress, the mean value for the free elastic component of the model ( $P_{R0}$ ) being 0.37% deformity (range 0.28–0.41%) for the two pooled samples (Table 1). The strain amplitudes of the two Maxwell elements ( $P_{R1}$  and  $P_{R3}$ ) had mean values of 0.18 and 0.15%, respectively, with relaxation time constants ( $P_{R2}$  and  $P_{R4}$ ) (i.e. times of maximal effect of each of the two elements) of 118.4 and 2.9 s, respectively (see Table 1). Thus, after an initial period of rapid free elastic recovery, the digesta subsequently recovered from the application of stress by the action of a fast Maxwell component, which is maximal at around 3 s after cessation of stress and a slower Maxwell component, which is maximal at around 100 s after cessation of stress. The durations of the latter two creep-recovery components were significantly different to that of the creep-compliance model describing response to externally applied shear strain, i.e.  $P_{R2}$  was significantly greater than  $P_{C2}$  (df 1.5,  $F=76.90$ ,  $P<0.0005$ ) and  $P_{R4}$  was significantly lower than  $P_{C2}$  (df 1.5,  $F=366.2$ ,  $P<0.0005$ ).

It is noteworthy that the residual strain following the initial elastic phase of creep recovery (0.37% deformation) was greater than that following the operation of the initial free elastic phase of creep compliance (0.16% deformation). This indicates that the stress energy stored in the elastic elements of the digesta is insufficient for complete recovery, i.e. there is a structural change, likely to be compaction, following creep-recovery. Further, the fact that the value of the relaxation time constant ( $\sim 40$  s) for the Kelvin element in the creep-compliance model differs from the values of the time constants ( $\sim 3$  and  $\sim 100$  s) of both the Maxwell elements in the creep-relaxation model indicates that the rheological characteristics also change following application of stress, likely as a result of extrusion of the liquid phase during compaction. Such extrusion can occur at two sites, first at the interstices between adjacent solid elements of digesta when creep-recovery is aided by the recovery of adjacent structures from elastic deformation; second within solid elements (e.g. the air spaces within leaves and plant stems) when recovery occurs mainly from the

operation of intrinsic elasticity within the walls of the element itself (e.g. the circumferential re-expansion of a plant stem causing re-establishment of the central air space). It is possible that the two Maxwell elements in the creep-relaxation model may represent the separate movement of the liquid phase at these two sites.

The fact that the linear portion of the creep-compliance curve commences only when the duration of period of application of the stress exceeds 100–150 s indicates that a significant period of Kelvin-type flow always precedes the establishment of simple viscous flow of digesta. Given the shortfall in recovery following the prolonged application of shear stress, it is evident that prolonged contractions that ‘knead’ colonic digesta (Davenport 1977) (i.e. initiate significant viscous flow and limited mixing) do so at the price of changing the flow properties of digesta (i.e. compacting the various elements of the solid phase).

However, the lack of any difference in the rheometric characteristics of the digesta from the proximal and distal colon indicates that the inherent elastic properties persist after passage through the proximal colon. This may indicate either that the durations of colonic contractions in the brushtail possum are insufficient to cause compaction of the solid phase or that there is restriction in the propagation of shear, and consequent viscoelastic flow, to the periphery of the digesta plug (Lentle et al. 2005). In the latter case, the application of shear, liquid phase extrusion and subsequent incomplete recovery is limited to successive peripheral annular segments of the plug of digesta as it traverses the colon.

No data are available describing the duration of contractions in the colon of the common brushtail possum. However, reported contractions of the more sustained type (Sarna 1985) in the isolated mouse colon (duration 26–45 s) (Fida et al. 1997), in the guinea pig colon (duration  $61.1 \pm 3.4$  s) (Smith et al. 2003) and in human subjects in vivo (Connell 1968) are of sufficient duration to span the duration of ‘Kelvin-type flow’ following application of stress. Further, the duration of contractions may increase with increase in the viscosity of digesta (Larson and Schultz 2002). Thus, it is likely that significant viscoelastic deformation of the digesta matrix and accompanying liquid displacement will occur during colonic contractions. Given that, in colonic peristalsis, a zone of relative dilatation precedes the zone of constriction (D’Antona et al. 2001), it is probable that liquid extruded from the digesta will pool in advance of the digesta plug and lubricate its progression in the manner postulated by Lentle et al. (2005).

The interval between successive contractions is long in isolated colon preparations (0.1–0.02 events per minute) (D’Antona et al. 2001). Such intervals provide adequate time for maximal recovery (i.e. the operation of both the fast and slow Maxwell elements). However, the interval between successive contractions decreases in preparations where a fixed bolus is positioned in the lumen (12.6–30.0 s between contractions) (Smith et al. 2003) (i.e. there is difficulty in initiating movement of

digesta). Peristaltic waves are known to occur at 30-second intervals in the human sigmoid colon, in runs of three to four contractions, each of 30 s duration (Connell 1968). In this situation, the duration of contraction will be sufficient to engage the operation of the Kelvin element in the creep-compliance curve and will cause liquid to be expressed from the digesta matrix. However, the intervals between successive contractions would be sufficient to span only the operation of the fast Maxwell element governing recovery. Thus, a proportion of extruded fluid may be driven either proximally or distally by successive colonic contractions. Indeed, in the case of retrograde peristalsis (Smith et al. 2003), this may allow some of the extruded liquid to be driven into the caecum in a manner that is analogous to the mechanism described by Björnhag (1987). A similar function may be served by rings of circular smooth muscle contraction of relatively short duration, travelling aborally and occurring with a frequency of around 30 s as observed in isolated guinea pig colon (D'Antona et al. 2001).

Incomplete reabsorption of the liquid phase of digesta in tubular components, when the contraction frequency exceeds the period required for recovery, may account for differences in the rate of passage of solid and liquid phase digesta markers in the tubiform forestomach of kangaroos and wallabies (Dellow 1982; Hume 1999) and the relative retention of the liquid phase in the hindgut of ringtail possums (Sakaguchi and Hume 1990; Hume and Moyle 1995). In this sense, the rheological properties of digesta may determine the overall frequency of intestinal contraction that is optimal for efficient reabsorption of extruded liquid phase and thus for efficient permeation of the digesta plug by digestive enzymes. It is tempting to speculate that interactions between neuronal stretch receptors (Spencer et al. 2002), smooth muscle tension (Spencer et al. 2001) and migrating motor patterns (Smith et al. 2003) may render colonic peristaltic rhythm and speed of propagation sensitive to the rheological characteristics of digesta, as has been indicated in the guinea pig ileum (Larson and Schultz 2002).

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