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## Diet switching in a generalist mammalian folivore: fundamental to maximising intake

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**Abstract** Generalist mammalian herbivores exploit a diverse diet. A generalised feeding strategy utilises a mixed diet to obtain a range of nutrients and to reduce the detoxication load of similar groups of plant secondary metabolites (PSMs). There is limited research investigating how mammalian herbivores achieve this dietary mixing in their daily foraging activities. We investigated the patterns of, and behaviours associated with, dietary mixing in a generalist mammalian folivore, the common brushtail possum (*Trichosurus vulpecula*). Possums were offered foliage of two eucalypt species (*Eucalyptus globulus* and *E. regnans*) as either (a) Full choice: both species offered for 8 h; (b) Restricted choice: both species offered for 2×2 h blocks; (c) G–R no choice: *E. globulus* offered for the first 4 h, *E. regnans* offered for next 4 h; and (d) R–G no choice: *E. regnans* offered for first 4 h, *E. globulus* offered for next 4 h. We hypothesised that possums would maximise intake on the Full choice diet, where time availability was greatest in combination with a choice of foliage. We also hypothesised that diet switching, defined as the frequency of changing between food types while feeding, would play a fundamental role in maximising intake. Possums achieved maximum intake on the Full choice diet and minimum intake on the No choice diets. Although

intake was similar between the Restricted choice and No choice diets, possums achieved this intake in half the amount of time when able to switch regularly between foliage on the Restricted choice diet. We conclude that a generalist herbivore's ability to effectively switch diets when foraging is fundamental to maximising intake. Hence, the degree of plant heterogeneity in an environment, and the spatial scale at which it occurs, may affect an herbivore's foraging decisions and, ultimately, influence its foraging efficiency.

**Keywords** Brushtail possum · Feeding behaviour · Mammalian herbivore · Plant secondary metabolite

### Introduction

Herbivores are continually challenged by dietary constraints including food availability and diet quality (i.e. nutrient and toxin content). The availability and quality of food can directly influence herbivore foraging decisions (Shipley and Spalinger 1995) and subsequently their habitat range (Cork and Pahl 1984; Lawler et al. 2000). To overcome these dietary constraints, herbivores have evolved feeding strategies that enable them to exploit their food source. These feeding strategies either specialise or generalise the foods that herbivores consume.

Specialist mammalian herbivores have adopted a feeding strategy that exploits a narrow diet range. This results in the ingestion of high levels of similar plant toxins, or plant secondary metabolites (PSMs). Specialists appear to subsist on this relatively homogenous diet by minimizing energy costs associated with ingesting these PSMs (Sorensen et al. 2005), and by efficiently metabolising and excreting them (Boyle et al. 1999). However, dietary specialisation in mammalian herbivores is relatively uncommon (Freeland 1991), and has been argued to be uncommon for two reasons. First, the nutrient constraint hypothesis argues that no one plant species can cater for all their nutrient demands (Westoby 1978).

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Second, the detoxification limitation hypothesis argues that mammalian herbivores are unable to detoxify large amounts of chemically similar PSMs (Freeland and Janzen 1974). Only when herbivores have evolved unique physiological traits to deal with low nutrient and high PSM ingestion are they able to specialise. An alternative, however, is to adopt a generalised feeding strategy.

Generalist mammalian herbivores exploit a diverse diet. This feeding strategy enables them to obtain a range of nutrients from a variety of plant species and to detoxify small concentrations of a chemically broad range of PSMs. As generalists cannot subsist on a single plant species, they must mix their diet to include plant species containing different nutritional and chemical properties. The benefit generalist herbivores derive from a choice of dietary species can be measured explicitly as a greater intake than with a single species. No choice diet (Freeland and Winter 1975; Dearing and Cork 1999; Wiggins et al. 2003). This act of dietary mixing is an important behaviour associated with maximising intake. Studies have been conducted on diet mixing in insect herbivores (e.g. Singer et al. 2002), but we are unaware of any that empirically test how a generalist mammalian herbivore mixes its diet during daily foraging activities.

The aim of this research was to determine which feeding patterns were associated with diet mixing in a generalist mammalian folivore, the common brushtail possum (*Trichosurus vulpecula*). By altering food availability and the time at which it was available, we tested whether and in what manner possums altered their feeding behaviour, and in which situation they were able to maximise intake. We used foliage from two eucalypt species, *Eucalyptus globulus* and *E. regnans*, which possums consume in their natural diet, and which differ in their chemical properties. We hypothesised that diet switching, defined as the frequency of changing between food types while feeding, was an important behaviour associated with maximising intake in a generalist mammalian folivore. We predicted that possums would maximise leaf intake under conditions in which they had the greatest opportunity to switch between food types over the longest possible feeding time.

## Materials and methods

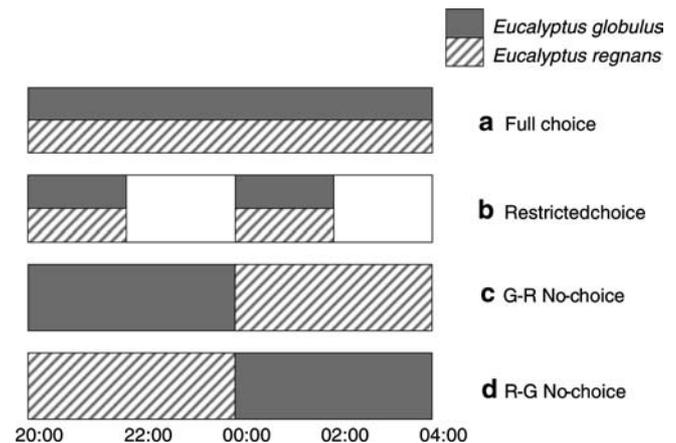
### Animals and diet

Eight adult brushtail possums (*T. vulpecula*), four males and four females (body weight mean  $3.7 \pm 0.6$  kg SD) were collected from Hobart (Tasmania, Australia). Possums were housed in individual mesh cages (4.3 m long, 1.7 m wide, 2.5 m high) in a covered outdoor enclosure at the School of Zoology, University of Tasmania. A nest box and logs were provided for each possum for environmental enrichment. Possums were maintained on a basal diet prepared fresh each day. The basal diet was 19% dry matter (DM) and consisted of (as % fresh matter, FM) 46% apple, 35% silver

beet, 10% carrot, 5% lucerne (ground to pass through a 1 mm sieve) and 4% raw sugar. Fresh diet constituents were mixed in a food processor and combined with dry ingredients. This diet was selected based on its similar nutritional content to some *Eucalyptus* foliage, one of the dominant plant genera consumed by wild brushtail possums in eastern Australia (Fitzgerald 1984). Possums were provided with fresh water daily, and food at levels sufficient for maintenance (McArthur et al. 2000).

### Feeding trial

Possums were initially fed their basal diet and *E. globulus* and *E. regnans* sapling foliage for 2 weeks before the trial. Foliage was collected from Geeveston, Tasmania and stored in a 5°C cooler room with stems in fresh water. For the feeding trial, possums were fed four treatment diets over 3 weeks in a cross-over design (Ratkowsky et al. 1993). The treatment diets were (a) Full choice: both species offered for 8 h; (b) Restricted choice: both species offered for 2×2 h blocks (no food was offered in-between the two 2 h blocks or for the last 2 h); (c) G–R no choice: *E. globulus* offered for the first 4 h, *E. regnans* offered for the next 4 h; and (d) R–G no choice: *E. regnans* offered for the first 4 h, *E. globulus* offered for the next 4 h (Fig. 1). Foliage was offered ad libitum as 200 g bunches. When foliage was offered simultaneously, it was separated by a distance of at least 1 m, to ensure that consumption of either species was easily observed. Each treatment was offered for three consecutive nights, with statistical analysis performed on



**Fig. 1** Diagrammatic representation of four treatment diets fed to brushtail possums, with time of night indicated at the base. Foliage was offered (a) simultaneously for eight consecutive hours in the Full choice treatment; (b) simultaneously for 2×2 h blocks in the Restricted choice treatment (total 4 h); (c) separately as *E. globulus* for the first 4 h, followed by *E. regnans* for the next 4 h in the G–R no choice treatment (total 8 h); and (d) separately as *E. regnans* for the first 4 h, followed by *E. globulus* for the next 4 h in the R–G no choice treatment (total 8 h). The potential to switch between diets was unlimited in (a) and (b), whereas, by definition, only one switch was possible in (c) and (d)

data from the third night. Each treatment was immediately followed by two 'rest' nights to ensure that possums maintained body weight during the trial.

### Foliage intake

Foliage intake was expressed as grams dry matter per kilogram of body mass for each possum (gDM kgBM<sup>-1</sup>). Leaves from control plants from each night were sub-sampled and either oven-dried at 55°C for 48 h to determine percentage dry matter, or frozen for later chemical analysis.

### Feeding behaviour

Behavioural data were measured for four possums by filming their nightly feeding activities. There was one camera per cage (B&W Bullet CCD Camera with Samsung™ sensor, JayCar, Hobart, Tasmania) with each camera connected to a Panasonic® Video Cassette Recorder (NV-FJ630 Series). Each cage contained an 80 W red flood lamp to enhance visibility (Osram Par 38, manufactured in EC). Video footage was recorded onto EMTEC BASF EQ-300 cassette tapes using long play. Filming started at 20:00 and ended at 04:00 the next morning. Data from video footage were summarised using The Observer® (v 4.1, Noldus Information Technology, The Netherlands, 2002).

The following behavioural variables were calculated from the video footage using The Observer® and Microsoft® Excel 2002 (Microsoft Corporation): (1) time from the first to last feeding bout (incorporating non-feeding activity); (2) total feeding time; (3) rate of intake; (4) number of feeding bouts; (5) time per feeding bout; (6) intake per feeding bout; (7) total number of visits to foliage; and (8) total number of switches. A single feeding bout was defined as the time from a possum's first bite to the end of its last chew, with at least one minute of non-feeding directly following this last chew. The number of visits to foliage was defined as a count of how many times possums visited each species of foliage, with possums able to visit more than one species more than once during a single feeding bout. This variable enabled comparisons of visits to foliage across all treatment diets. The total number of switches was a count of switches between species while feeding, and could occur both within and between feeding bouts during a night. Switching behaviour could only be compared between the choice diet treatments (a) and (b).

### Foliage chemistry

Two control bunches of foliage per species per night were sub-sampled for each analysis. Foliage was assayed in duplicate for each night of the experiment for

nitrogen, fibre and total oils. Foliage was assayed in duplicate for nights one and three of each treatment for total phenolics, due to logistical constraints.

For nitrogen and fibre analyses, foliage was oven-dried at 55°C for 48 h and ground to pass through a 1 mm sieve using a cyclone grinder.

**Nitrogen** Foliage samples were further oven-dried at 70°C for 24 h prior to the nitrogen digest. A sulphuric acid and hydrogen peroxide digest was performed following Lowther (1980). Digested samples were then colorimetrically analysed for nitrogen (QuikChem reference 10-107-06-2E, Lachat Instruments, Wisconsin, USA) on a continuous flow injector analyser (QuikChem 800, Lachat Instruments). Results are expressed as % DM.

**Fibre** Plant cell-wall components of neutral detergent fibre, acid detergent fibre, lignin and ash were determined following procedures outlined in the ANKOM<sup>200/220</sup> Technology Operator's Manual, 1997. Results are expressed as % DM.

Fresh-frozen foliage was thawed before oil and phenolic analyses were performed.

**Total oils** Oils were extracted using dichloromethane with heptadecane as an internal standard, following methods modified from Jones et al. (2002). One gram of foliage was cut into ~1 cm<sup>2</sup> pieces and soaked in 10 ml dichloromethane for 1 h. Extracts were analysed by combined gas chromatography–mass spectrometry (GC–MS), detailed in O'Reilly-Wapstra et al. (2004). Total ion currents were determined for the sum of all oil components (total oils) and the heptadecane internal standard. Results for total oils were then standardised by dividing by the internal standard. Results are expressed as mg 'cineole equivalents' per gram DM.

**Total phenolics** Phenolics were extracted using acidified (pH 1) methanol (Close et al. 2001). One gram of foliage was cut into ~1 cm<sup>2</sup> pieces and homogenised using a Polytron Homogenizer (POLYTRON® MR2100, Kinematica AG, Switzerland) in 20 ml acidified methanol and boiled for ~1.5 min. Samples were extracted overnight at 5°C in the dark. Extracts were centrifuged at 10,000 rpm for 7 min, and analysed by high-performance liquid chromatography (HPLC), detailed in O'Reilly-Wapstra et al. (2004). A value for total phenolics could not be calculated, as we could not chromatographically quantify chemically different compounds between *E. globulus* and *E. regnans*, as each compound had its own unique response factor.

Representative chromatograms of oils and phenolics of *E. globulus* and *E. regnans* foliage were used as a visual reference to demonstrate differences in PSM composition between the two species (see Figs. 4, 5).

## Statistical analyses

Intake data for all eight possums and behavioural data for four possums from day three were used in the analyses. Dependent variables of intake and aspects of feeding behaviour were tested against the independent variables of possum, treatment, period and carryover, using the General Linear Model Procedure (Proc GLM, SAS v6.12, SAS Institute Inc. 1990), following Ratkowsky et al. (1993). As the effect of carryover was never significant, it was removed from the final models. The Wilk–Shapiro statistic, normal probability plots and plots of the standardised residuals all indicated normality of the data. When an effect was significant, pairwise comparisons of least-squares means were made using the Tukey–Kramer adjustment. Paired *t* tests between the foliar chemical properties of *E. globulus* and *E. tenuiramis* were performed to test for differences in chemistry using the Univariate Procedure (Proc Univariate, SAS Institute Inc. 1990).

## Results

### Intake and feeding behaviour

Possums tended to consume more foliage when it was offered as a Full choice diet than on the Restricted and No choice diets ( $F_{3, 31} = 2.56$ ;  $P = 0.08$ ; Fig. 2). The

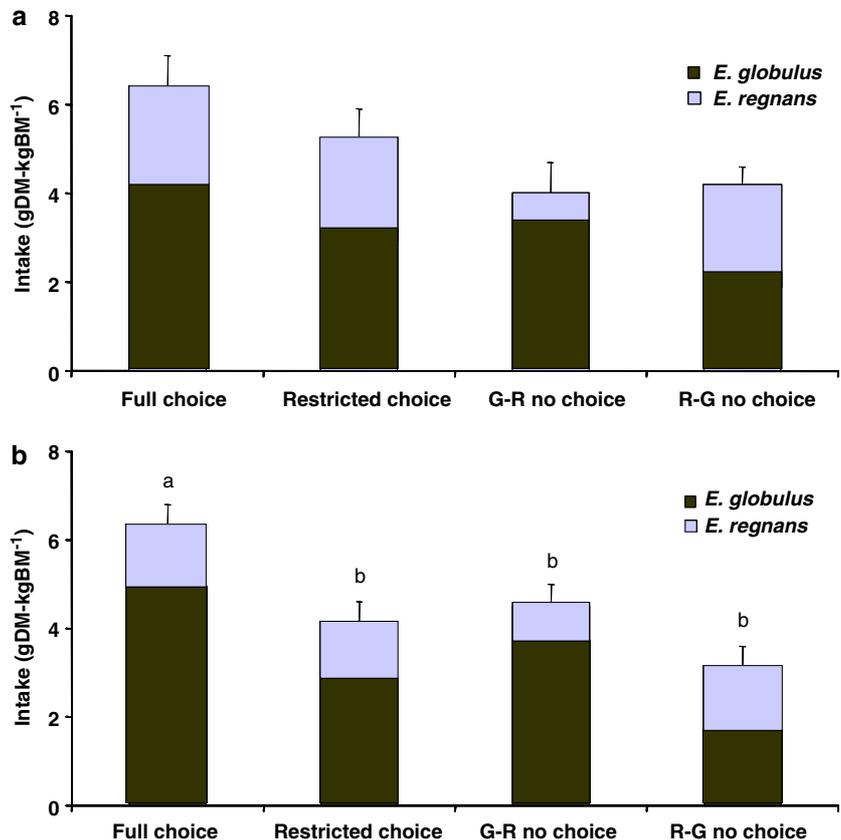
four possums from which behavioural data were collected consumed significantly more foliage on the Full choice diet than on all other diets ( $F_{3, 15} = 7.39$ ;  $P = 0.02$ ; Fig. 2).

Possums visited *E. globulus* and *E. regnans* foliage more often ( $F_{3, 15} = 9.84$ ;  $P = 0.01$ ) and increased their rate of intake ( $F_{3, 15} = 7.17$ ;  $P = 0.02$ ) on the Full choice treatment than on other treatments (Fig. 3). Possums switched between the two species more frequently on the Full choice diet ( $28 \pm 1.4$ ) than the Restricted choice diet ( $18 \pm 1.4$ ) ( $F_{1, 7} = 10.09$ ;  $P = 0.05$ ). Possums did not alter their time from the first to last feeding bout ( $5.6$ – $6.5$  h;  $P = 0.62$ ), total feeding time ( $29.1$ – $36.8$  min;  $P = 0.41$ ), number of feeding bouts ( $15.8$ – $24.8$ ;  $P = 0.14$ ), intake per feeding bout ( $0.19$ – $0.29$  gDM kgBM<sup>-1</sup>·bout<sup>-1</sup>;  $P = 0.21$ ), or show any clear pattern of time per feeding bout ( $1.5$ – $2.3$  min·bout<sup>-1</sup>;  $P = 0.07$ ) in response to treatment diets.

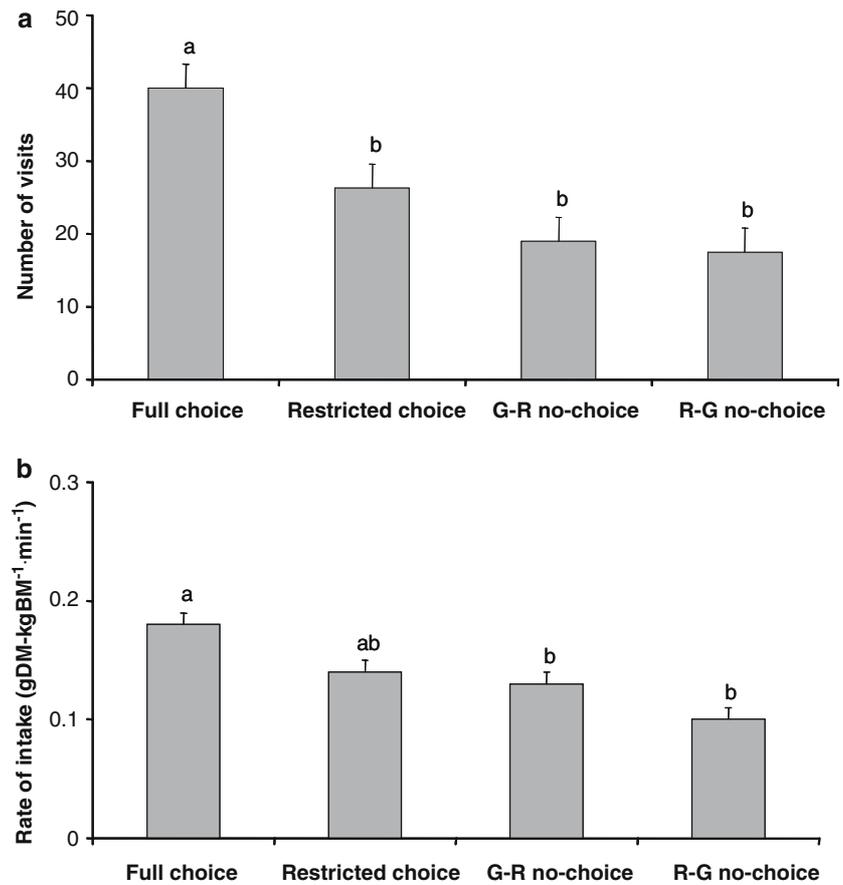
### Foliage chemistry

Leaf percentage dry matter (DM) and fibre components were all greater in *E. regnans* than *E. globulus*, but there was no difference in nitrogen levels (Table 1). *E. regnans* had a 24% greater oil yield than *E. globulus* and there were no similarities between the major oil compounds identified for the two species (Table 1; Fig. 4). Total phenolic composition between

**Fig. 2** Total intake (gDM·kgBM<sup>-1</sup>) of *E. globulus* and *E. regnans* foliage by (a)  $n = 8$ ; and (b)  $n = 4$  of these brushtail possums across diet treatments. Values are least-squares means with *s.e.* bars. Letters that differ are significantly different ( $\alpha = 0.05$  after Tukey–Kramer adjustment for multiple comparisons)



**Fig. 3** Results showing (a) total number of visits to; and (b) rate of intake ( $\text{gDM}\cdot\text{kgBM}^{-1}\text{min}^{-1}$ ) of *E. globulus* and *E. regnans* foliage by brushtail possums across diet treatments. Values are least-squares means with *s.e. bars*. Letters that differ are significantly different ( $\alpha=0.05$  after Tukey–Kramer adjustment for multiple comparisons)



*E. globulus* and *E. regnans* was also substantially different (Fig. 5).

## Discussion

The common brushtail possum, *T. vulpecula*, was able to maximise intake when *E. globulus* and *E. regnans* foliage was offered simultaneously for eight consecutive hours. When foliage availability was reduced through time constraints, or available for 8 h but not offered simultaneously, possums were unable to maintain intake. Possums reduced their visits to foliage, number of

switches between foliage (when switching option was available) and their rate of intake in response to constraints in availability of the plants.

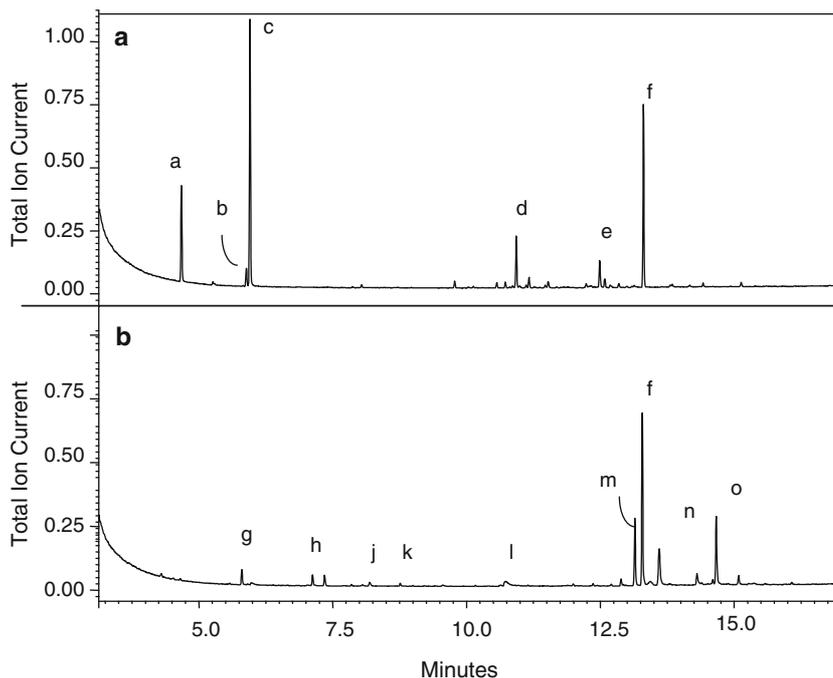
The secondary metabolite composition (i.e. total oils and total phenolics) of *E. globulus* and *E. regnans* foliage differed markedly, both quantitatively and qualitatively (Table 1; Figs. 4, 5). These differences were sufficient enough that possums were able to increase intake while diversifying PSM intake through dietary mixing (Freeland and Janzen 1974). We have previously found that *T. vulpecula* benefits more from diet mixing, as they ate 16 g of foliage on a choice diet of *E. globulus* and *E. regnans*, but only 10 and 6 g,

**Table 1** Chemical constituents of sapling foliage of *E. globulus* and *E. regnans* fed to brushtail possums

Constituent	Units	<i>Eucalyptus globulus</i>	<i>Eucalyptus regnans</i>	Paired <i>t</i> test	
				Mean difference	<i>P</i> value
Dry matter	% DM	39.7 ± 2.1	55.1 ± 5.5	-15.9 ± 12.4	< 0.01
Nitrogen	% DM	1.4 ± 0.0	1.4 ± 0.0	-0.02 ± 0.2	0.70
NDF	% DM	33.4 ± 0.8	37.6 ± 1.3	-5.3 ± 6.9	< 0.01
ADF	% DM	22.0 ± 0.5	30.2 ± 1.0	-0.8 ± 4.5	< 0.01
Lignin	% DM	10.0 ± 0.5	18.9 ± 0.9	-9.4 ± 2.7	< 0.01
Ash	% DM	0.3 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	0.04
Total oils	Cineole equivalents (mg g DM <sup>-1</sup> )	18.6 ± 1.7	24.6 ± 5.6	-10.8 ± 31.8	0.20

*n* = 12 and *n* = 11 for *E. globulus* and *E. regnans*, respectively  
NDF is neutral detergent fibre; ADF is acid detergent fibre

**Fig. 4** Representative chromatograms of (a) *E. globulus* and (b) *E. regnans* oils derived from combined gas chromatography–mass spectrometry (GC–MS). Compounds are labelled with assigned letters, which stand for (a)  $\alpha$ -pinene; (b) limonene; (c) 1,8-cineole; (d) aromadendrene; (e) globulol; (f) *n*-heptadecane (internal standard); (g) *p*-cymene; (h) *cis*-*p*-menth-2-en-1-ol; (i) *trans*-*p*-menth-2-en-1-ol; (j) piperitol; (k) piperitone; (l) 4-hydroxybenzeneethanol; (m)  $\beta$ -eudesmol; (n) tasmanone; (o)  $\beta$ -eudesmyl acetate



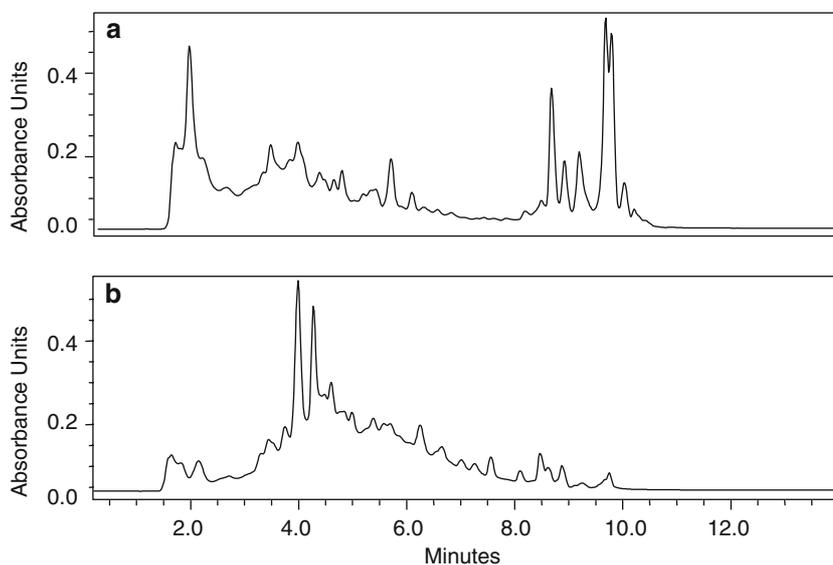
respectively, when offered only *E. globulus* or *E. regnans* as a single species No choice diet (N.L. Wiggins and C. McArthur, unpublished data).

All treatment diets offered to possums enabled them to mix their diets during their nightly foraging activities. However, the way in which this diet mixing could be achieved varied and this in turn affected how much foliage they were able to consume. When foliage was present for eight consecutive hours, intake was higher when possums were able to frequently diet switch between the two species, than when possums could only diet switch once during the No choice diet (when diets were alternated at 4 h). When foliage was available for only half the amount of time (4 h), possums consumed

similar amounts as the No choice diets. However, this intake was achieved in only half the amount of available foraging time. The capacity to frequently switch diets therefore offers some benefit enabling possums to consume foliage in a reduced timeframe.

The nutrient constraint hypothesis proposes that a mix of dietary foods provides the best source of different important nutrients that an animal requires (Westoby 1978). However, due to the short-term nature of this experiment, and the similar nitrogen levels between *E. globulus* and *E. regnans*, we propose that diet switching was not an immediate response to nutritional constraints of the diets. Consistent with this, Singer et al. (2002) demonstrated that diet switching in the caterpillar

**Fig. 5** Representative total phenolic profiles for (a) *E. globulus* and (b) *E. regnans* using high-performance liquid chromatography (HPLC) chromatograms at 280 nm. Previous studies (e.g. O'Reilly-Wapstra et al. 2005) have helped us identify the chromatogram peaks between 8 and 10.5 min in *E. globulus* as predominately formylated phloroglucinol compounds (FPCs), known herbivore feeding deterrents. Analysis of *E. regnans* has revealed that many of the peaks in this 8–10.5 min region are not FPCs



*Grammia geneura*, a generalist insect herbivore, was not affected by plant primary nutrient qualities of the diet, but rather by plant secondary metabolite qualities. We propose that frequently switching between foliage within the timeframe of minutes or hours during feeding provides additional benefits related to coping with PSMs.

Plant secondary metabolite ingestion appears to be governed by some critical threshold (Pfister et al. 1997; Pass and Foley 2000), so that rate of detoxification and thus elimination are important in determining how much an herbivore can eat per unit of time (Freeland 1991). Therefore, the consumption of several chemically different plant species should provide a range of PSMs that can be metabolised through the use of several different rate-limited detoxification pathways (Freeland and Janzen 1974). By actively switching between two chemically different species, *E. globulus* and *E. regnans*, both during and between nightly feeding bouts, we suggest that possums are overcoming the short-term intake constraint due to toxic effects of each species. This switching behaviour enables possums to continue feeding on one species (e.g. *E. regnans*) during intervals when they cannot consume the other species (e.g. *E. globulus*) due to detoxification limitations (Fig. 6). This satisfactorily explains why possums achieved maximum intake when both plant species were available for eight consecutive hours, and why they experienced reduced intake on all other diets.

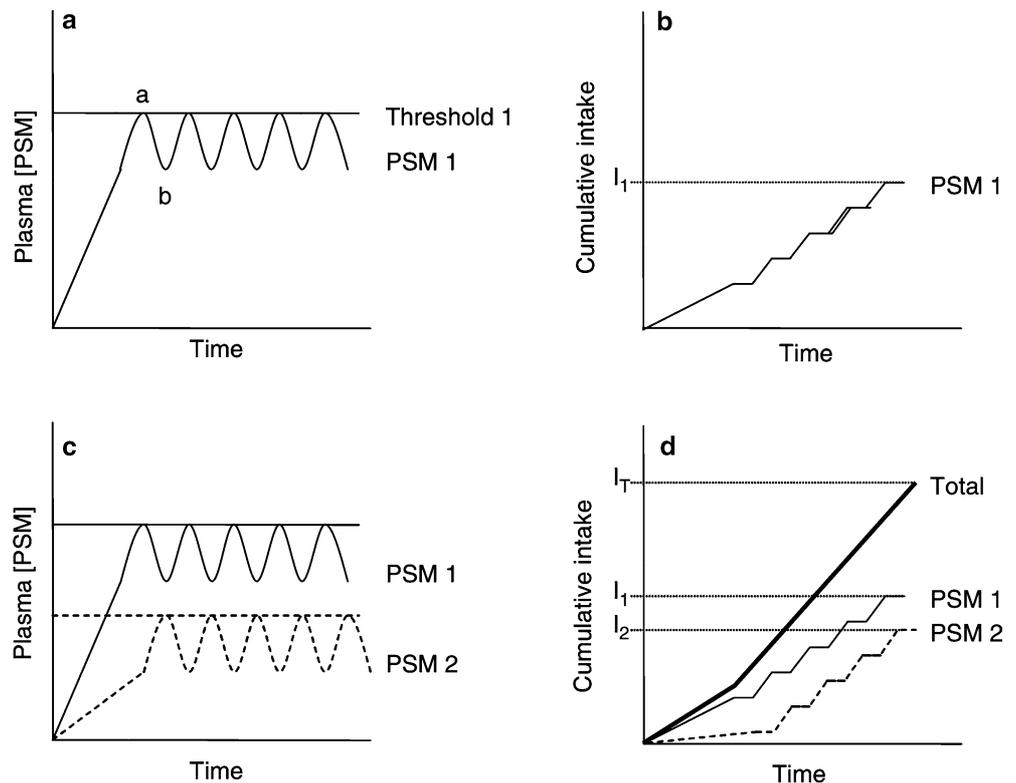
Partial support for adopting, and indeed benefiting from, diet switching as a feeding behaviour may be taken from a recent captive trial. When possums were

presented with two chemically different eucalypts as a distinct 'patch', they foraged four times more efficiently than when the two eucalypts were presented as two distinct patches, separated by a distance of 70 m (N.L. Wiggins et al., unpublished manuscript). These results suggest that diet switching, at a scale relevant to impose foraging costs, is an important behaviour associated with maximising intake, and thus foraging efficiency, in brushtail possums.

Diet switching may explain why possums were able to achieve maximum intake, but our results also demonstrate how, from a behavioural perspective, this occurred. That is, concurrent with switching between plant species, possums were able to visit and consume foliage more frequently and at a quicker rate. These feeding behaviours have consistently been shown as important indicators of how both the common ringtail possum (*Pseudocheirus peregrinus*) (N.L. Wiggins et al., unpublished manuscript) and common brushtail possum alter their intake in response to diet (Wiggins et al. 2003).

Field studies have shown that brushtail possums select particular habitats within their home range when foraging at night (le Mar and McArthur 2005), but there are no studies investigating foraging patterns by possums on a finer spatial (tree by tree) or temporal scale. Our results, however, clearly demonstrate that diet switching, presumably at a frequency relevant to the detoxification rates of the PSMs being consumed, plays a fundamental role in maximising intake in generalist mammalian herbivores such as brushtail possums (Fig. 6). From this, we predict that such herbivores

**Fig. 6** Hypothetic model of diet mixing by a generalist herbivore. Figure 1a shows plasma PSM concentrations of an herbivore consuming PSM 1, obtained from diet source one. As plasma concentration for PSM 1 reaches a threshold (point *a*), intake stops until it is reduced, through detoxification, below this threshold. Once plasma concentration is at a safer level (point *b*), intake may resume again. This effect of feeding pattern on intake is shown in Fig. 1b. When PSM 2, obtained from diet source two and chemically different to PSM 1, is introduced into the model (Fig. 1c), an herbivore may consume PSM 2 during non-feeding intervals of PSM 1 as in Fig. 1d. Total intake is greater when an herbivore switches regularly between chemically different diet sources



will be able to maximise intake, and ultimately foraging efficiency, in an environment in which plant heterogeneity occurs at a spatial scale appropriate to enable effective switching between food types.

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