PLANT-ANIMAL INTERACTIONS

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Sideroxylonal in *Eucalyptus* foliage influences foraging behaviour of an arboreal folivore

Abstract Plant secondary metabolites (PSMs) offer plants chemical defences against herbivores, and are known to influence intake and diet choice in both insect and mammalian herbivores. However, there is limited knowledge regarding how PSMs influence herbivore foraging decisions. Herbivore foraging decisions, in turn, directly impact on which individual plants, and plant species, are selected for consumption. We took advantage of the natural variation in sideroxylonal concentrations in the foliage of *Eucalyptus melliodora* (Cunn. ex Schauer) to investigate feeding patterns of a marsupial folivore, the common ringtail possum, *Pseudocheirus peregrinus* (Boddaert 1785). Foliage, collected from six trees, contained between 0.32 and 12.97 mg g-DM^{-1} sideroxylonal. With increasing sideroxylonal concentrations, possums decreased their total intake, rate of intake and intake per feeding bout, and increased their cumulative time spent feeding. Possums did not alter their total feeding time, number of feeding bouts or time per feeding bout in response to increasing sideroxylonal concentrations. Results demonstrate important behavioural changes in foraging patterns in response to sideroxylonal. These behavioural changes have important implications, in relation to altered foraging efficiency and potential predation risk, for herbivores foraging in the field. As a result, the spatial distribution of dietary PSMs across a landscape may directly influence herbivore fitness, and ultimately habitat selection of mammalian herbivores.

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Plant secondary metabolites (PSMs) are chemical compounds produced by plants that are proposed to play a defensive role against herbivores (Fraenkel 1959; Freeland and Janzen 1974). Various PSMs have been shown to reduce intake in a range of herbivores, including winter moth larvae, *Operophtera brumata* (Feeny 1970), desert woodrats, *Neotoma lepida* (Meyer and Karasov 1989), cattle (Pfister et al. 1997), and a range of marsupials (Foley et al. 2004). PSMs have also been shown to affect diet choice in mammalian herbivores (e.g. McArthur et al. 1993; Dearing and Cork 1999; Wiggins et al. 2003). Herbivores can detect dietary PSMs using both pre-ingestive (i.e. smell or taste) (Pass and Foley 2000) and post-ingestive (i.e. negative feedback, conditioned flavour aversions) (Provenza 1995; Lawler et al. 1998a, b) processes. These physiological processes initiate the behavioural response of altered food intake (Provenza et al. 1992). By reducing their intake in response to dietary PSMs, herbivores can minimise the detrimental effects that PSMs pose, such as toxicity (Pfister et al. 1997), acidosis (Foley 1992) and digestibility reduction (Robbins et al. 1987).

While the effects of PSMs on intake and diet choice are often well known, there has been limited research on the relationship between dietary PSMs and foraging patterns of herbivores. Foley et al. (1999) described a preliminary model, based on proposed detoxification and elimination rates of a model PSM, to predict the feeding strategies that herbivores could adopt when ingesting dietary PSMs. If PSM ingestion depends on detoxification limitations in mammalian herbivores (Freeland and Janzen 1974), then patterns of ingestion should depend on an herbivore's detoxification and elimination rates. Taking these into account, Foley et al.

(1999) demonstrated that herbivores could maintain maximum rates of food intake in response to increasing levels of PSMs simply by adjusting feeding bout duration and non-feeding intervals.

Understanding the importance of changes in foraging patterns in response to dietary PSMs requires detailed empirical studies. In one such study supporting the detoxification limitation hypothesis, Wiggins et al. (2003) showed that common brushtail possums, *Trichosurus vulpecula*, decreased their feeding rate and decreased their feeding bout size, with increasing concentrations in an artificial diet of the terpene, cineole. There have been few studies on feeding patterns using PSMs in natural foliage diets. The exceptions are recent studies on invertebrates including grasshoppers (Bernays et al. 1994) and caterpillars (Singer et al. 2002). All showed that PSMs influence feeding behaviour.

Eucalyptus contains a range of PSMs that can vary greatly between and within species (Hillis 1966; Li et al. 1995, 1996; Eschler et al. 2000; Wallis et al. 2002). Research on the interaction between eucalypt chemistry and mammalian herbivores initially focused on terpenes and phenolics (e.g. Foley 1992). Another chemical group, the formylated phloroglucinol compounds (FPCs), was described more recently (Eschler et al. 2000). The FPCs have been shown to have a major influence on feeding by marsupial folivores (Lawler et al. 1998a; Eschler et al. 2000; Stapley et al. 2000). It is well known that the arboreal folivores, the common ringtail and common brushtail possum, eat less with increasing concentrations of FPCs (Lawler et al. 2000; Wallis et al. 2002; Wallis and Foley 2002; O'Reilly-Wapstra et al. 2004). However, it is not known how FPCs affect the feeding patterns, and subsequently the foraging decisions, of mammalian herbivores.

In this study, we took advantage of the natural variation in FPCs between individual trees of *Eucalyptus mclliodora* to examine how one such compound, sideroxylonal, affects the feeding behaviour of the common ringtail possum, *Pseudocheirus peregrinus*. Based on the hypothesis that the detoxification of PSMs drives herbivore-feeding patterns, we predicted that, as with brushtail possums fed cineole (Wiggins et al. 2003), ringtail possums would decrease both their rate of intake and intake per feeding bout. These alterations in feeding behaviour may subsequently minimise the negative effects of ingested dietary PSMs.

Materials and methods

Six adult ringtail possums, four males and two females, body weight mean 0.85 ± 0.07 kg (SD), were collected from areas surrounding the Australian National University, Canberra. Possums were housed in individual cages (1.8 m$\times$2.0 m$\times$3.2 m) in a covered outdoor enclosure at the School of Botany and Zoology, and were thus subjected to natural variation in day length and temperature. Possums were maintained on *Eucalyptus rossii* foliage, a favoured species locally, and a basal diet prepared fresh each day. The basal diet consisted of (percent fresh matter, FM) 53% apple, 27% banana, 9.4% ground lucerne, 5.3% ground bran, 4% crushed Weet-Bix™ (Sanitarium™, Berkeley Vale, NSW, Australia), 1% acid casein (NZMP Ltd., Wellington, New Zealand) and 0.3% vitamin/mineral supplement (Min-A-Vit®, Souter's™, Huntingwood, NSW, Australia). The diet was 23.8% dry matter (DM). All fruit and vegetable matters were mixed in a food processor then combined with the dry ingredients. Possums were provided with 300 g of fresh food, which exceeded their maintenance energy requirements.

Feeding trial

Six treatment diets were fed to six possums over 12 days based on a Latin square design. The treatment diets consisted of adult foliage from six individual trees of *E. melliodora*, collected from Canberra and surrounding areas. Trees were selected based on their estimated sideroxylonal concentrations from near infrared reflectance spectroscopy (Rose Andrews, personal communication), which were expected to range from 0 to 20 mg sideroxylonal g-DM^{-1}. An upper limit of 20 mg g-DM^{-1} sideroxylonal was chosen based on how much ringtail possums ate in previous feeding trials (e.g. Lawler et al. 2000). We sought mature foliage as sideroxylonal values had previously been estimated from adult foliage, but due to limited availability, used younger foliage from one tree. Foliage was presented to possums in bunches weighing about 100 g (FM). Possums received a treatment diet one night, immediately followed by a 'rest night' when they received 300 g of basal diet and foliage of *E. rossii*. This design enabled us to observe how sideroxylonal affected possum feeding behaviour while minimising weight loss and reducing carryover effects between treatments (Lawler et al. 1998a, b).

Intake was measured as dry matter (g DM). Dry matter intake (DMI) of the foliage diet was calculated for each possum as follows: Percentage dry matter (% DM) of the diets offered was obtained by oven-drying a sub-sample of the diet at 55°C for 48 h. This was used to convert FM offered into DM offered. Any remaining diet and spillage (orts) were collected the next morning and weighed, and then the orts were oven-dried at 55°C for 48 h. Individual intakes were then calculated as the DM offered minus the DM remaining.

Behavioural analysis

Possums were filmed each night that they received a treatment diet. Filming started at 17:00 and ended at 08:00 the next morning, with one camera per cage. Each camera was connected to a Panasonic® Video Cassette Recorder (NV-FJ600 and NV-FJ630 Series). Video footage was recorded directly onto EMTEC BASF EQ-300 cassette tapes using extended long-play. Data from

video footage were summarised using The Observer® (v 3.0, Noldus Information Technology, The Netherlands, 2002).

The following variables were calculated from the behavioural observations using The Observer and Microsoft® Excel 97 (Microsoft Corporation, Redmond, WA, USA): (1) time from the start of the first to the end of the last feeding bout (including non-feeding activity); (2) total feeding time; (3) rate of intake (DMI/feeding time); (4) number of feeding bouts; (5) time per feeding bout (feeding time/bout); and (6) intake per feeding bout (DMI/bout). A single feeding bout was defined as the time between a possum starting to feed and stop feeding for at least 1 min. An additional variable, cumulative feeding time, was calculated as the progressive sum of feeding time, plotted against time of night (h) to establish a visual pattern of nightly time spent feeding (Fig. 1). For each possum on each treatment (tree), we estimated the time taken to complete 20% of their total feeding time. This value was standardised against the feeding time for the foliage with the lowest concentration of sideroxylonal, which thus acted as the control. A value of 20% was chosen as most possums fed for the equivalent of 20% of the total feeding time they spent on the control foliage. A value such as 50% of total cumulative feeding time could not be used, as in many cases, possums did not feed for long enough on the high sideroxylonal treatment diets to compare a value with the control diet. This variable enabled us to standardise the data and compare between treatments, in order to determine whether possums shifted their nightly cumulative feeding patterns in response to sideroxylonal concentration.
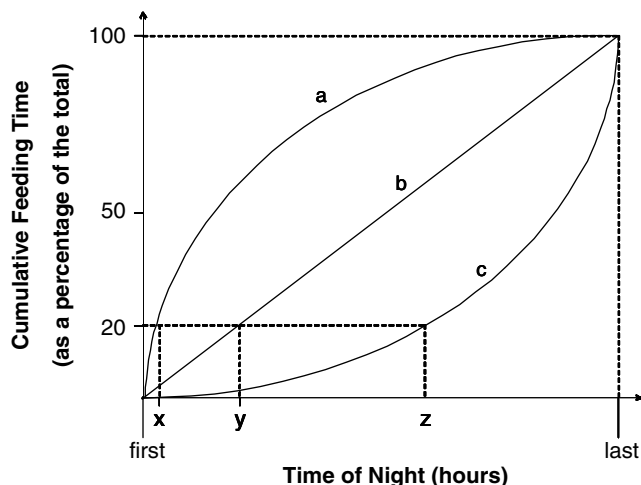

Fig. 1 Graphical model of cumulative feeding time, showing three possible nightly feeding patterns. The x-axis is the time of night in hours, where 'first' is time zero, when an animal first starts feeding, and 'last' is the animal's last feeding activity. The y-axis is the cumulative time spent feeding. Curve a illustrates most feeding activity early on; curve b a regular feeding pattern; and curve c with little feeding early on. The letters x, y and z correspond to the 20th percentile for curves a, b and c, respectively. Note that as feeding activity changes from early (a) to regular (b) to late (c), the time of night for the 20th percentile value increases (x to z)

Foliage analysis

Six control bunches of foliage, from each of the six different treatment diets fed to *P. peregrinus*, were used for foliage analysis. Foliage was freeze-dried and then ground to pass through a 1-mm sieve. It was assayed in duplicate for nitrogen, fibre, total phenolics and sideroxylonal.

Plant primary chemistry

Nitrogen

Sub-samples of the foliage were oven dried at 70°C for 24 h prior to digestion. A sulphuric acid–hydrogen peroxide digest was performed following the methods of Lowther (1980). Digested samples were then colorimetrically analysed for nitrogen (QuikChem reference 10-107-06-2E, Lachat Instruments, Miluwakee, WI, USA) on a continuous flow injector analyser (QuikChem 800, Lachat Instruments).

Fibre

Plant cell-wall components of neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin were measured following methods in the ANKOM[200/220] Technology Manual (1997).

Plant secondary chemistry

Sideroxylonal

Sub-samples of the foliage were analysed following the methods of Wallis et al. (2003) to determine total sideroxylonal concentrations.

Total phenolics

Sub-samples of the foliage were extracted in 70% acetone in preparation for total phenolic assays, following the procedures outlined in Hagerman (1995). Total phenolics were assayed following the modified Prussian blue assay for total phenolics (Graham 1992), using gallic acid as a standard.

Statistical analysis

Pearson's correlation coefficients were calculated (PROC CORR, SAS v 6.12, SAS Institute Inc. 1990) between all foliage chemical constituents in order to determine the extent to which effects on feeding patterns, attributed to sideroxylonal, were independent of other compounds. Dependent variables of DMI and aspects of feeding behaviour were first tested against the explanatory variables of tree (treatment), sex, period and carryover, using the General Linear Model

Procedure (PROC GLM, SAS Institute Inc., Cary, NC, USA) following procedures of Ratkowsky et al. (1993). The Wilk–Shapiro statistic, normal probability plots and plots of the standardised residuals all indicated normality of the data. If the tree effect was significant, a univariate regression analysis (PROC REG, SAS Institute Inc., Cary, NC, USA) was then performed on the least-squares means to establish the nature of the relationship with the concentration of sideroxylonal, as sideroxylonal was the most dominant explanatory variable. If a curvilinear relationship was suggested by the data, the line of best fit was chosen using square root or log transformation of the dependent variable. We plotted and expressed all data in terms of concentration of sideroxylonal for six trees used in the trial.

Results

Foliage chemistry

The six *E. melliodora* varied in their foliage chemistry but sideroxylonal showed by far the greatest range in concentration (40-fold) compared with a maximum two-fold range for the other compounds (Table 1). The fibre measures (NDF, ADF and lignin) were all strongly correlated to one another ($r = 0.99$), and were all negatively but less strongly correlated with sideroxylonal (e.g. NDF $r = -0.74$; Table 2). Nitrogen and total phenolics were also negatively correlated with sideroxylonal but to a lesser degree ($r = -0.50$ and -0.32, respectively; Table 2).

Dry matter intake

Possums ate markedly different amounts depending on which of the six *E. melliodora* was the source of the foliage (range 3.6–32.8 g-DM; $F_{5,35} = 13.33$; $P < 0.001$). Sideroxylonal concentration explained 85% of variation in intake and was best described by a negative exponential relationship (Fig. 2).

Time from first to last feeding bout and total feeding time

Individual *P. peregrinus* spread their feeding bouts over 7.4–8.2 h (incorporating non-feeding activity) and this was unaffected by the treatment tree ($F_{5,35} = 0.68$; $P = 0.65$). Of this time, they spent between 0.4 and 1.1 h actually feeding. Again, treatment tree did not affect the time spent feeding ($F_{5,35} = 1.16$; $P = 0.37$).

Rate of intake

Possums ate foliage of individual trees at different rates (0.06–0.81 g-DM min^{-1}; $F_{5,35} = 7.24$; $P < 0.001$) (Fig. 3). In general, with increasing concentrations of sideroxylonal, *P. peregrinus* decreased their rates of intake, but this appeared to be a stepped relationship. There was a dramatic reduction (66%) in rate of intake from the tree with the lowest concentration of sideroxylonal (0.32 mg g-DM^{-1}) to that with the second lowest concentration (2.18 mg g-DM^{-1}). The rate of intake was then stable at approximately 0.37 g-DM min^{-1} up to a sideroxylonal concentration of 9.7 mg g-DM^{-1}, before a further reduction in the rate of intake at the highest sideroxylonal concentration (Fig. 3).

Number of feeding bouts

Pseudocheirus peregrinus had between 11 and 20 feeding bouts per night, but this did not depend on the tree they were fed ($F_{5,35} = 1.60$; $P = 0.21$).

Intake per feeding bout and time per feeding bout

The tree that possums were offered determined how much they ate in each feeding bout (0.4–2.8 g-DM bout^{-1}; $F_{5,35} = 6.92$; $P < 0.001$) and as with intake, this was a negative exponential relationship (Fig. 4). Each feeding bout lasted between 1.4 and 4.0 min, independent of the tree *P. peregrinus* was feeding from ($F_{5,35} = 1.22$; $P = 0.19$).

Table 1 Primary and secondary foliage chemistry and intake by *Pseudocheirus peregrinus* of six individual *Eucalyptus melliodora* trees. For each tree, $n = 2$ for chemistry, $n = 6$ for intake. Values are expressed as means $\pm$ SE

	Unit	Tree 1 BM33	Tree 2 KM5	Tree 3 MS17	Tree 4 MS5	Tree 5 MS84	Tree 6 MS30	Ratio
Nitrogen	% DM	1.4 ± 0.0	1.8 ± 0.0	1.5 ± 0.0	1.1 ± 0.0	1.3 ± 0.0	1.4 ± 0.0	1:1.6
NDF	% DM	28.3 ± 0.1	26.0 ± 0.4	21.2 ± 0.1	24.7 ± 0.5	22.9 ± 1.0	23.1 ± 0.4	1:1.3
ADF	% DM	22.0 ± 0.4	19.2 ± 0.4	14.9 ± 0.3	17.6 ± 0.3	15.9 ± 0.5	17.0 ± 0.3	1:1.5
Lignin	% DM	11.0 ± 1.2	9.1 ± 0.6	6.3 ± 0.1	8.6 ± 0.8	7.4 ± 0.3	7.8 ± 0.2	1:1.7
Total phenolics	mg GA g-DM^{-1}	56.3 ± 2.7	32.5 ± 1.1	51.6 ± 2.1	45.8 ± 2.1	43.6 ± 0.0	36.6 ± 1.9	1:1.7
Sideroxylonal[a]	mg g-DM^{-1}	0.3	2.2	6.9	8.9	9.7	13.0	1:43.3
Foliage intake[b]	g-DM	32.8 ± 2.8	13.7 ± 3.0	15.5 ± 3.0	9.5 ± 2.9	7.5 ± 3.1	3.6 ± 3.0	

Ratio refers to the ratio of lowest:highest concentrations for each compound
% DM percentage dry matter, *NDF* neutral detergent fibre, *ADF* acid detergent fibre, *GA* gallic acid
[a]Values averaged from samples with a coefficient of variation $< 5\%$
[b]Foliage intake is expressed as least-squares means (g-DM)

Table 2 Pearson's correlation coefficients between mean levels of all foliage primary and secondary chemistry in *Eucalyptus melliodora* foliage from six trees used in feeding trials. Significance at $P < 0.05$ is indicated in bold

	Nitrogen	NDF	ADF	Lignin	Phenolics
NDF	0.13				
ADF	0.17	**0.99**			
Lignin	0.05	**0.99**	**0.99**		
Total phenolics	−0.42	0.15	0.18	0.20	
Sideroxylonal	**−0.50**	**−0.74**	**−0.73**	**−0.69**	−0.32

NDF neutral detergent fibre, *ADF* acid detergent fibre

Cumulative feeding time

With increasing sideroxylonal concentrations, *P. peregrinus* took longer to complete 20% of their total cumulative feeding time compared with that on the lowest sideroxylonal concentration diet ($F_{5,31} = 4.76$; $P = 0.04$; Fig. 5).

Discussion

Our results indicate that sideroxylonal in *E. melliodora* foliage significantly influenced intake of foliage and feeding behaviour of the common ringtail possum, *P. peregrinus*. We do not believe that fibre, which of the other compounds analysed, showed the strongest (negative) correlation with sideroxylonal, affected the results of this study. This negative relationship with sideroxylonal was also associated with a negative relationship with intake it seems unlikely that possums would reduce their intake in response to decreasing fibre levels. In addition, the 40-fold range in sideroxylonal concentration covered levels known to influence intake (Lawler et al. 2000), while the range of NDF concentration was much narrower.

Possums ate less with increasing concentrations of sideroxylonal in foliage. This is consistent with previous studies that tested the effects of sideroxylonal in both

Fig. 2 Dry matter intake (g-DM) of *E. melliodora* foliage by *P. peregrinus* as a function of sideroxylonal concentration (mg g-DM^{-1}). Values are least-squares means $\pm$ SE bars. The equation of the line is: $DMI = e^{(-0.14[sideroxylonal] + 3.38)}$, $r^2 = 0.85$, $n = 6$, $P = 0.01$
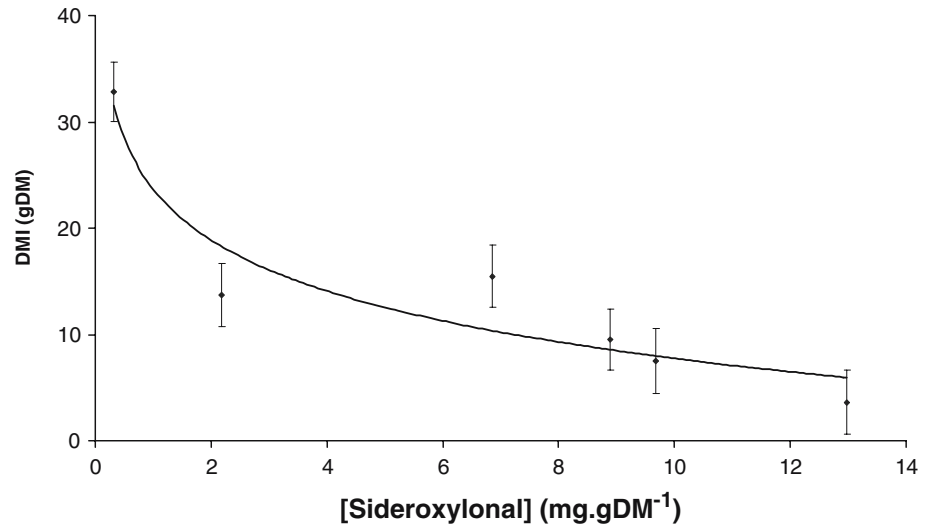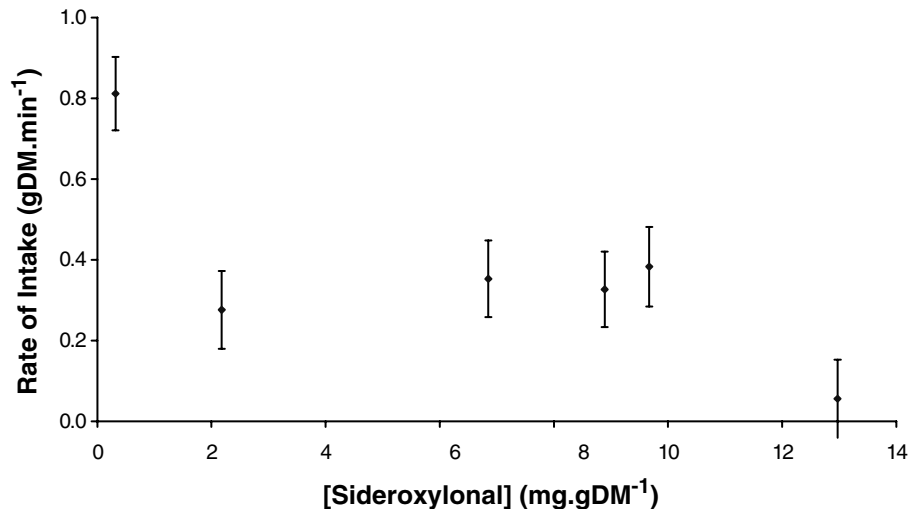

Fig. 3 Rate of intake (g-DM min^{-1}) of *E. melliodora* foliage by *P. peregrinus* as a function of sideroxylonal concentration (mg g-DM^{-1}). Values are least-squares means $\pm$ SE bars

Fig. 4 Intake per feeding bout (g-DM bout^{-1}) of *E. melliodora* foliage by *P. peregrinus* as a function of sideroxylonal concentration (mg g-DM^{-1}). Values are least-squares means ± SE bars. The equation of the line is: DMI bout^{-1} = e$^{(-0.18[\text{sideroxylonal}] + 0.90)}$, $r^2 = 0.86$, $n = 6$, $P = 0.01$
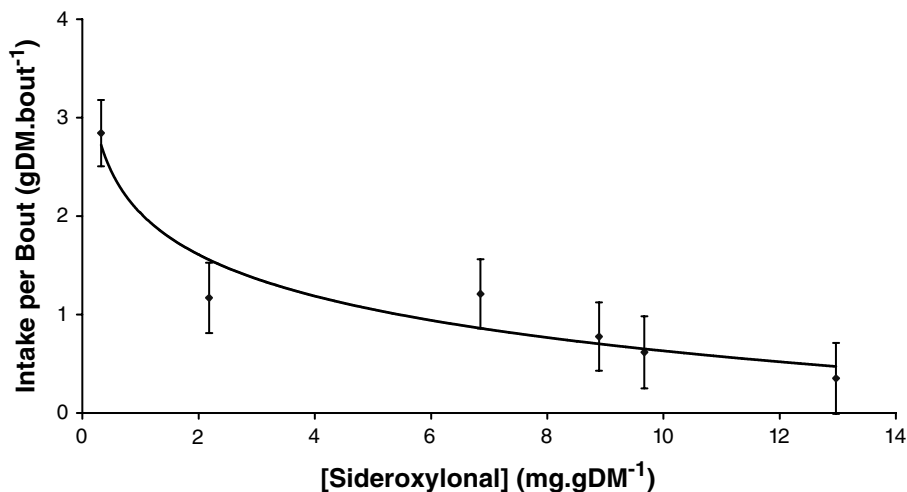
artificial and foliage diets fed to both ringtail and brushtail possums (Lawler et al. 2000; Wallis et al. 2002; Wallis and Foley 2002; O'Reilly-Wapstra et al. 2004). Our results further demonstrate that reduced intake by ringtail possums was associated with behavioural changes in feeding (summarised in Fig. 6). As sideroxylonal concentrations increased, *P. peregrinus* maintained the same number of feeding bouts, the duration of these bouts, their total feeding time and the total duration of time used for feeding. However, when food intake is accounted for, possums ate less per feeding bout in a negative exponential relationship, and reduced their rate of intake in a negative stepped relationship. They also shifted their cumulative feeding patterns during the night, taking longer on the two highest sideroxylonal concentrations to complete the equivalent of 20% of their total feeding time on the control foliage.

Ringtail possums responded to sideroxylonal in much the same way as brushtail possums did to an artificial diet with increasing cineole concentrations (Wiggins et al. 2003). Brushtail possums decreased intake, intake per feeding bout and rate of intake. These similar

behavioural responses by two different folivorous species to different PSMs in both artificial and natural diets, suggest that behaviour is an important regulator of PSM intake (Wiggins et al. 2003).

Previous work has shown that herbivores can regulate PSM intake (Pfister et al. 1997; Lawler et al. 1998b; Stapley et al. 2000; Boyle and McLean 2004). This regulation appears to be governed by their physiological threshold to a particular PSM. If this threshold is reached or even overshot, consumption of the PSM ceases until the animal is able to detoxify and thus reduce the concentrations in its body, below the threshold level (Pfister et al. 1997). If animals are not capable of tightly regulating their intake of PSMs, then detrimental effects are likely (i.e. toxicity, acidosis, internal malaise) (Foley 1992; Provenza 1995; Pfister et al. 1997). It is known that ringtail possums fed on an artificial diet can regulate sideroxylonal intake from day-to-day (Lawler et al. 2000). Although this regulatory ability appeared to be poorer when the same animals were fed foliage containing sideroxylonal, the authors suggested that intake in any given feeding bout may be important for

Fig. 5 Cumulative feeding time of *E. melliodora* foliage, expressed as the time taken for *P. peregrinus* to perform 20% of their total cumulative feeding time compared with foliage with the lowest concentration of sideroxylonal, as a function of sideroxylonal concentration (mg g-DM^{-1}). Values are means for six possums ± SE bars
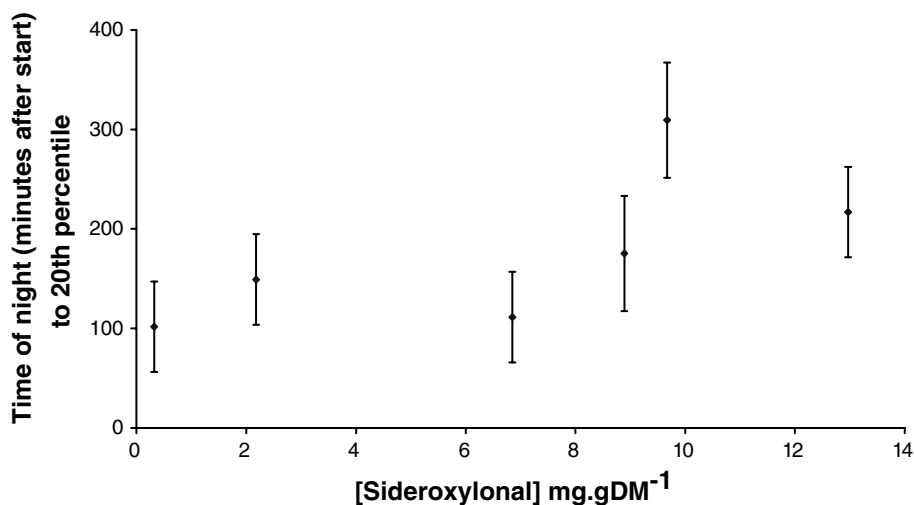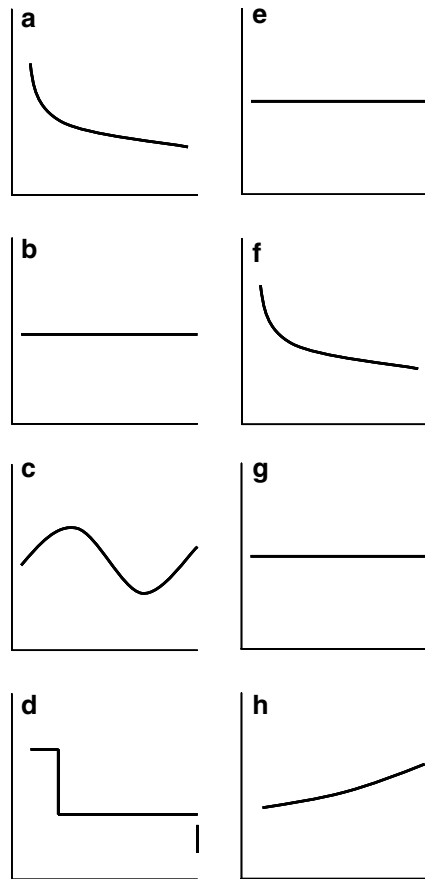
Fig. 6 Summary of results for *P. peregrinus* fed *E. melliodora* foliage showing patterns of **a** dry matter intake; **b** time from first to last feeding bout; **c** total feeding time; **d** rate of intake; **e** number of feeding bouts; **f** intake per feeding bout; **g** time per feeding bout; and **h** cumulative feeding time. The *x*-axis represents sideroxylonal concentration

regulating sideroxylonal intake below the critical threshold (Lawler et al. 2000). Results of our current study support the idea that possums are able to regulate sideroxylonal intake, and that feeding bout size is indeed an important behaviour associated with this regulatory ability. Our results further indicate that a reduction in feeding rate and extended patterns of cumulative feeding time are other important regulatory behaviours by which possums regulate sideroxylonal ingestion. We did not find that bout frequency or duration was affected by increasing toxin concentrations, contrary to the predictions of Foley et al. (1999). This may have been the result of possums having less frequent and much shorter feeding bouts than the values used in their model. In addition, the behavioural patterns shown by possums represent just one possible feeding strategy for dealing with increasing toxin concentrations, which is also addressed by Foley et al. (1999). Our results do provide support for the idea that behavioural regulation of PSM ingestion is important, through rate of ingestion, which may be related to herbivore detoxification and elimination rates (Foley et al. 1999).

The short-term behavioural responses to dietary sideroxylonal by ringtail possums have important implications for free-ranging possums. Reduced nightly intake due to sideroxylonal was the net effect of reduced rate of intake and feeding bout size, along with delayed cumulative feeding time. Thus, sideroxylonal incurs behavioural as well as intake costs. It is clear that in their natural environment, possums must make crucial foraging decisions. Possums foraging in the wild are likely to encounter a range of dietary PSMs, which will directly influence their foraging behaviours (e.g. Fig. 1), and subsequently, their foraging decisions. If possums choose to tolerate reduced intake as a result of the negative effects of dietary PSMs, they risk reduced nutrient consumption. Alternatively, possums could try to increase intake through diet mixing (Dearing and Cork 1999; Wiggins et al. 2003), or use a combination of these strategies. Diet mixing is likely to directly affect foraging costs because it would require the animal to move further and to shift between plants more often (Wiggins et al., unpublished manuscript). Thus, selecting a different food source in between bouts of feeding on high sideroxylonal foliage may increase both energetic costs of foraging and the risk of predation, ultimately impacting on herbivore fitness. The spatial heterogeneity of plant (food) species, and the scale at which this occurs across a landscape, may therefore prove a crucial factor affecting foraging on trees and shrubs. This, in turn, will directly impact on habitat selection of individual animals, in response to dietary PSM properties. Results highlight the potential impact that plant–herbivore interactions can impose on both plant and herbivore.

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